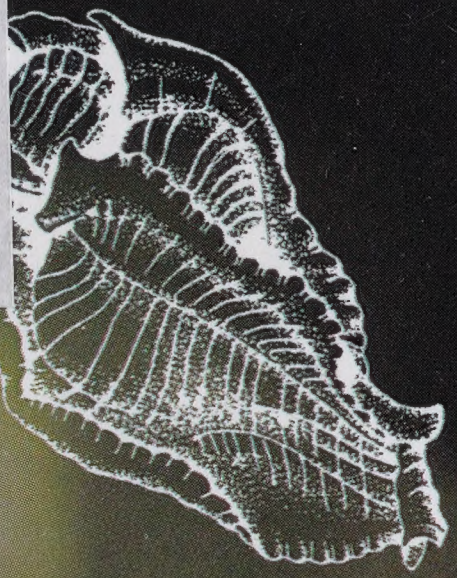


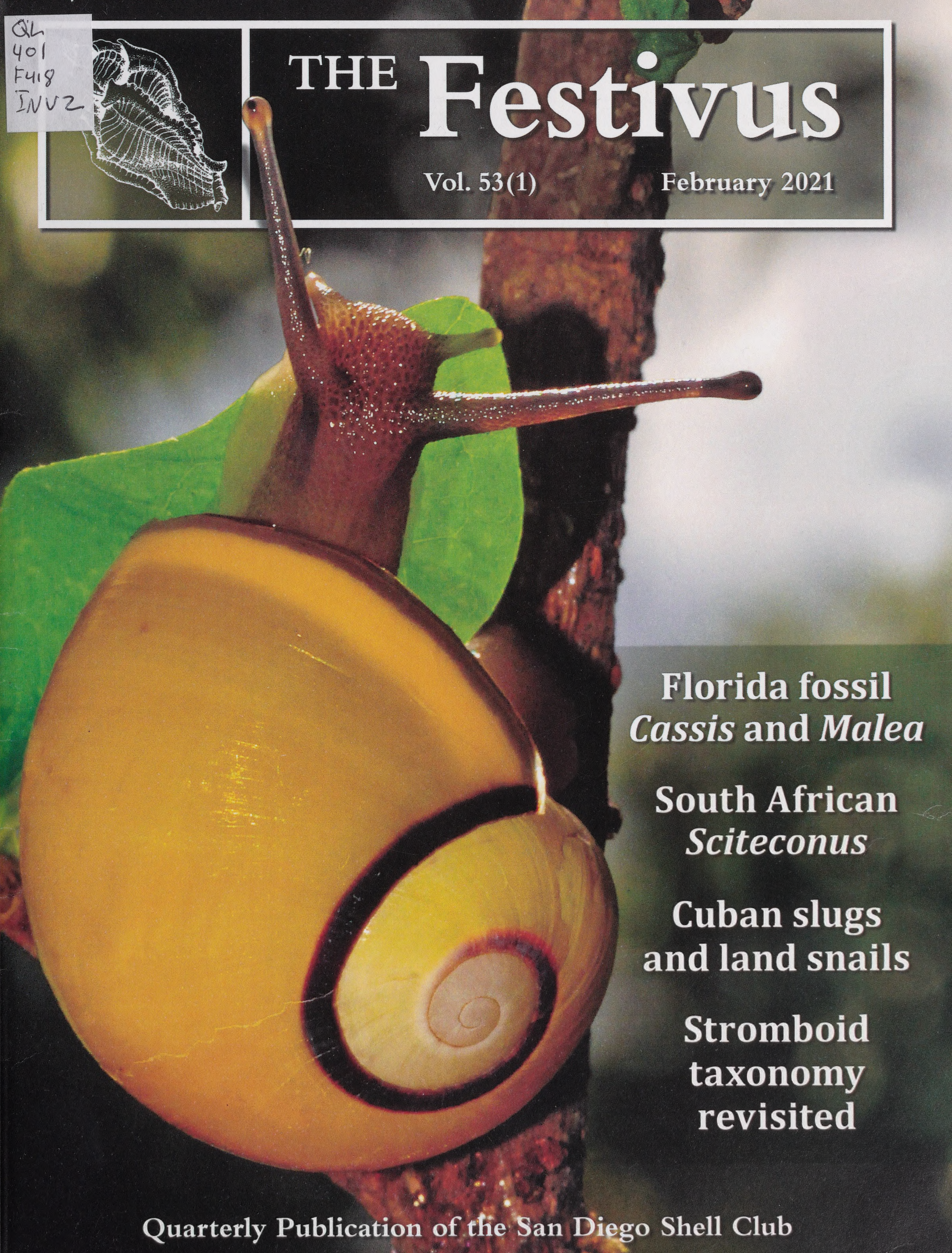
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THE Festivus

Vol. 53(1)

February 2021



Florida fossil
Cassis and *Malea*

South African
Sciteconus

Cuban slugs
and land snails

Stromboid
taxonomy
revisited

Quarterly Publication of the San Diego Shell Club



THE FESTIVUS

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February 2021

ISSUE 1

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FRONT COVER:

Photograph of *Polymita venusta* color form *nigrosuturalis* by Adrián González-Guillén at an abandoned chicken farm, La Luz vicinity, San Luis municipality, Santiago de Cuba province, Eastern Cuba. (Cover artistic credit: Rex Stilwill).

MISSION STATEMENT

The San Diego Shell Club was founded in 1961 as a non-profit organization for educational and scientific purposes. More particularly to enjoy, study and promote the conservation of Mollusca and associated marine life through lectures, club meetings and field trips. Our membership is diverse and includes beginning collectors, scientists, divers, underwater photographers and dealers.

THE FESTIVUS is the official quarterly publication of the San Diego Shell Club, Inc. and is issued as part of membership dues in February, May, August and November. *The Festivus* publishes articles that are peer reviewed by our volunteer Scientific Peer Review Board, as well as articles of general interest to malacologists, conchologists, and shell collectors of every level. Members of the Peer Review Board are selected to review individual articles based upon their chosen field of expertise and preference. Available by request or on our website are:

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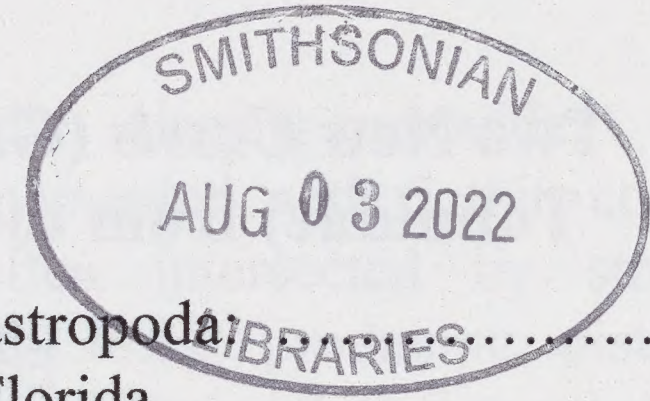
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April 17, 2021 - 1:00 p.m. "Save the Abalone!" event, potluck, and shell auction featuring shells from the Krattli legacy collection.

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Editor's Note: *The Festivus* is accepting articles for future issues. Articles of a scientific nature may be submitted for the peer reviewed portion of our journal. Please refer to our Guidelines for Authors, and/or Guidelines for the Description of New Taxa in *The Festivus*, both available on our website: <http://www.sandiegoshellclub.com/festivus/>.

Two New *Cassis* (Gastropoda: Cassidae) and a New *Malea* (Gastropoda: Tonnidae) from the Pliocene and Pleistocene Beds of Southern Florida

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ABSTRACT Two new fossil Helmet Shells of the genus *Cassis* Scopoli, 1777 (Cassidae) and a new fossil Grinning Tun Shell of the genus *Malea* Valenciennes, 1832 (Tonnidae) are described from the Pliocene and Pleistocene fossil beds of southern Florida. The new Helmet Shells, *Cassis rasae* n. sp. and *Cassis viliusi* n. sp., were both collected in the rich fossil beds of the Holey Land Member of the Bermont Formation (Calabrian Stage, Early Pleistocene) and the new Grinning Tun, *Malea hyaducki* n. sp., was collected in the Fruitville Member (Kissimmee River Valley equivalent beds) of the Tamiami Formation (late Piacenzian Stage of the Pliocene). The discovery of two new large Helmet Shells in the Holey Land Member demonstrates that four species of *Cassis* are present in the Bermont Formation, making this the single largest fossil *Cassis* fauna found anywhere on Earth. The new Grinning Tun represents the oldest-known *Malea* found in Florida, and is the direct ancestor of the Gelasian Pleistocene *Malea springi* (Caloosahatchee Formation) and the Calabrian Pleistocene *Malea petiti* (Bermont Formation).

KEY WORDS *Cassis*, *Cassis rasae*, *Cassis viliusi*, *Malea*, *Malea hyaducki*, Bermont Formation, Tamiami Formation, Calabrian Stage, Pleistocene Epoch, Piacenzian Stage, Pliocene Epoch

INTRODUCTION

Although quite rare in the worldwide fossil record, large Helmet Shells of the genus *Cassis* are relatively common in the Holey Land Member of the Bermont Formation of southern Florida. Here, four *Cassis* species are now known to have occurred sympatrically during the Calabrian Stage of the Early Pleistocene, making this the single richest fossil *Cassis* fauna known from anywhere on Earth. The four large Bermont Helmet Shells, which include *Cassis schnireli* Petuch, 1994, *C. jameshoubricki* Petuch, 2004, and two new species that are described here, were apparently predators of the extremely rich fauna of echinoids that is characteristic of the Holey Land Member (found in the paleoecosystem of

the “*Titanostrombus williamsi* Community”; see Petuch, 2004: 230-233). In contrast to the relative abundance of large cassids in the Bermont Formation, the tonnid genus *Malea* is rarely found in the fossil beds of southern Florida and is known from only a few specimens in private and museum collections. Three species are currently known from southern Florida; *Malea petiti* Petuch, 1989 from the Holey Land Member of the Bermont Formation, *M. springi* Petuch, 1989 from the Fort Denaud Member of the Caloosahatchee Formation, and an unnamed Late Pliocene species (previously misidentified as “*Malea densecostata*” and described here) from the Fruitville Member of the Tamiami Formation.

The authors are currently in the process of completing the first comprehensive overview of the paleontology, stratigraphy, paleoceanography, and paleogeography of the Everglades region of Florida ("Ancient Seas of Southern Florida", CRC Press) and the new cassid and tonnid taxa described here will be included within the upcoming book. The holotypes of the two new *Cassis* species and the new *Malea* are deposited in the molluscan type collection of the Paleontological Research Institution (hereinafter "PRI"), Ithaca, New York and bear PRI catalog numbers.

SYSTEMATICS

Class Gastropoda

Subclass Sorbeoconcha

Order Prosobranchia

Infraorder Mesogastropoda

Superfamily Tonnoidea

Family Cassidae

Genus *Cassis* Scopoli, 1777

Cassis rasae Petuch and Berschauer,
new species
(Figures 1A, B)

Description. Shell of average size for genus, averaging around 200 mm in length, elongated and narrow, with only slightly inflated body whorl; spire proportionally high and elevated, distinctly subpyramidal; shoulder sharply angled, with sharply-sloping subsutural areas; shoulder ornamented with 10-14 proportionally-large, sharply-pointed knobs; body whorl ornamented with 2 rows of smaller, less-developed knobs, one around anterior one-third of body whorl and one around mid-body, with each row having 8-12 low, rounded knobs; areas between rows of smaller knobs ornamented with 4-6 strong, wide, low cords, with smaller secondary cords between pair of larger cords; anterior area of body whorl, between row of knobs and siphonal canal, ornamented with 6-8

thin, strong cords; sloping shoulder and subsutural area ornamented with 5 thin cords; shoulder cords often intersected by strong longitudinal growth lines, producing distinct fenestrate sculpture pattern; siphonal canal short, narrow, recurved dorsally; parietal shield roughly triangular in shape, with rounded sides, often preserving original central color patch (such as on holotype, Figure 1B); columellar area of parietal shield ornamented with 20-30 thin, elongated teeth, arranged in parallel, that are longer and better developed on anterior half; aperture proportionally narrow, widening toward the anterior end; outer lip wide and flattened, ornamented with 10-12 large, widely-separated pointed teeth, with middle teeth being largest and best developed, extending into aperture.

Type Material. HOLOTYPE - Length 165.2 mm, width 108.4 mm, Holey Land Member of the Bermont Formation, Loxahatchee, Palm Beach County, Florida, PRI 13346; OTHER MATERIAL EXAMINED - Three specimens, lengths 246 mm, 220 mm, and 192 mm, from the same locality as the holotype.

Type Locality and Stratigraphic Range. The holotype was collected from the lowest beds in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida. The new species is confined to the lower beds of the Holey Land Member, Bermont Formation, Calabrian Stage of the Early Pleistocene.

Etymology. Named for Rasa Petuch of Vilnius, Lithuania, daughter-in-law of the senior author.

Discussion. Of the four known *Cassis* species found in the Holey Land Member, *Cassis rasae* is the smallest and also has the most elongated body whorl and highest spire. The new species is morphologically closest to *C. schniireli* Petuch, 1994 (Figures 1G, H), but differs in being a

smaller, far less inflated, less rounded, and more protracted species, in having larger, fewer, and better developed knobs on the shoulder and body whorl, and in having a higher, more pyramidal spire.

Cassis viliusi Petuch and Berschauer,
new species
(Figures 1C, D)

Description. Shell of average size for genus, averaging around 150 mm in length, inflated and barrel-shaped, triangular in shape; spire proportionally low, broadly pyramidal; shoulder sharply angled, subcarinate, with sharply-sloping subsutural areas; shoulder edge ornamented with 17-20 small, closely-packed, sharply-pointed knobs; body whorl ornamented with 2 rows of smaller, poorly-developed, almost obsolete knobs, one around anterior one-third of body whorl and one around mid-body, with each row having 15-20 low, rounded knobs; areas between rows of smaller knobs ornamented with 5-6 strong, wide, low cords, with smaller secondary cords between pair of larger cords; anterior area of body whorl, between row of knobs and siphonal canal, ornamented with 6-8 thin, wider and more flattened cords; shoulder and subsutural area ornamented with 4-5 thin cords; early whorls of spire heavily ornamented with 4 rows of large, prominent rounded beads; siphonal canal short, narrow, recurved dorsally; parietal shield broad and expanded, oval in shape, often preserving original central color patch (such as on holotype, Figure 1D); columellar area of parietal shield ornamented with 35-40 thin, elongated teeth, arranged in parallel rows, with smaller secondary ribs often present between pairs of larger ribs; aperture proportionally narrow, widening toward anterior end; outer lip wide and flattened, ornamented with 10 large, widely-separated pointed teeth, with middle 4

teeth being largest, best developed, and with flattened, bifurcated ends.

Type Material. HOLOTYPE - Length 169.5 mm, width 115.1 mm, Holey Land Member of the Bermont Formation, Loxahatchee, Palm Beach County, Florida, PRI 13348; OTHER MATERIAL EXAMINED - Two specimens, lengths 176 mm and 139 mm, from the same locality as the holotype.

Type Locality and Stratigraphic Range. The holotype was collected from the lowest beds in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida. The new species is confined to the lower beds of the Holey Land Member, Bermont Formation, Calabrian Stage of the Early Pleistocene.

Etymology. Named for Vilius Vaičiulis of Vilnius, Lithuania, an inspired young naturalist and student of science.

Discussion. Of the four known *Cassis* species found in the Holey Land Member, *Cassis viliusi* most closely resembles *C. schnireli* Petuch, 1994 (Figures 1G, H), but differs in having a more inflated shell with a distinctly triangular shape and lower spire, in being a smoother, less ornamented shell that lacks strong cords and pronounced rows of knobs on the body whorl, and in having more numerous and proportionally smaller knobs along the shoulder.

Family Tonnidae

Genus *Malea* Valenciennes, 1832

Malea hyaducki Petuch and Berschauer,
new species
(Figures 2A, B)

Description. Shell of average size for genus, averaging around 100 mm, thin, inflated, globose, bulliform, with rounded shoulder; spire

elevated, subscalariform, broadly pyramidal, with deeply incised sutures; body whorl smooth and shiny, encircled by 18-20 wide, low, flattened, equally-spaced spiral cords; aperture wide and flaring, distinctly crescent-shaped; columellar area with deep, prominent rectangular notch along anterior one-third; columellar notch bordered by pair of large prominent knobs, with each knob bearing 3 large blade-like teeth; smaller, less-developed elongated pustules present along entire columella and on edge of parietal shield, particularly anterior end; parietal shield proportionally large and expansive, covering approximately three-quarters of shell base, with prominent recurved edge along anterior end; outer lip wide and flattened, ornamented with 20 large, evenly-spaced narrow ribs, with each terminating in small rounded tooth within edge of aperture.

Type Material. HOLOTYPE - Length 120 mm, width 90.6 mm, Fruitville Member of the Tamiami Formation, Rucks Pit, Fort Drum, Okeechobee County, Florida, PRI 13349; OTHER MATERIAL EXAMINED - (fragmentary, missing the outer lip) length 91 mm, from the same locality as the holotype.

Type Locality and Stratigraphic Range. The holotype was collected from the lowest beds of the Rucks Pit (Fort Drum Crystal Mine), Fort Drum, Okeechobee County, Florida. The new species is confined to the Fruitville Member of the Tamiami Formation, late Piacenzian Stage of the Late Pliocene.

Etymology. The new tonnid is named for Harry J. Hyaduck, Sr. of Atlanta, Georgia, an inspired amateur paleontologist who collected the holotype in the Rucks Pit and generously donated it to the senior author for further study.

Discussion. This large and distinctive Floridian *Malea* was first found by Olsson and Petit, who illustrated it in their 1964 paper on new Pliocene and Pleistocene mollusks that had been uncovered in canal excavations around Lake Okeechobee. Although representing the first *Malea* species found in Florida, they erroneously referred this large and impressive tonnid to the taxon *Malea densecostata* (Rutsch, 1934) from the Punta Gavilan Formation of Venezuela (Zanclean Stage, Early Pliocene). That older Gatunian Paleoprovince South American species differs from the younger late Piacenzian Stage North American *Malea hyaducki* in being a much more narrow and elongated shell with finer and more numerous spiral ribs on the body and spire whorls and in having a proportionally lower spire. The teeth on the outer lip of *M. densecostata* are also more numerous, stronger, and better developed than those seen on the new Floridian species. Of the two other known Floridian species, *Malea hyaducki* is closest to *M. springi* Petuch, 1989 (Figures 2C, D) from the Gelasian Stage Fort Denaud Member of the Caloosahatchee Formation. The new Tamiami Formation species differs from its younger Early Pleistocene descendant species in being a smaller, thinner, and more inflated shell with a proportionally-higher spire, and in having fewer cords on the body and spire whorls. The outer lip of the Caloosahatchee *M. springi* is also wider and has much more numerous and stronger teeth that extend into the aperture (readily seen here by comparing Figures 2B with 2D).

Fossil *Cassis* and *Malea* Species known from the Pliocene and Pleistocene Formations of Southern Florida (Okeechobee Group of Formations)

Only around 20 species of Helmet Shells of the genus *Cassis* are known from fossil beds around

the world (Petuch and Berschauer, 2018). Of these, 9 are only known from the fossil beds of southern Florida, demonstrating that the Okeechobean Sea (the paleosea that flooded the Floridian Peninsula during the late Neogene Period) was the center of *Cassis* evolution for the entire Western Atlantic Region (Tucker & Wilson, 1932; Petuch, 2004; Petuch and Roberts, 2007). Here, large *Cassis* species have been found to be abundant in several of the formations of the Okeechobee Group (all the carbonate-rich formations of southern Florida, including the Tamiami, Caloosahatchee, Bermont, and Fort Thompson Formations; see Petuch and Roberts, 2007). These are arranged here chronologically and stratigraphically and include:

Piacenzian Stage, Late Pliocene: 3.6-2.58 mya

Tamiami Formation, Pinecrest Member

Cassis floridensis Tucker and Wilson, 1932

Tamiami Formation, Fruitville Member

Cassis ketteri Parodiz and Tripp, 1992

Gelasian Stage, Early Pleistocene: 2.58-1.8 mya

Caloosahatchee Formation, Fort Denaud Member

Cassis calusa Petuch and Berschauer, 2018

Caloosahatchee Formation, Ayers Landing Member

Cassis powelli Petuch and Berschauer, 2018

Calabrian Stage, Early Pleistocene: 1.8 mya-780,000

Bermont Formation, Holey Land Member

Cassis jameshoubrieki Petuch, 2004 (Figure 1E, F)

Cassis rasae Petuch and Berschauer, n. sp. (Figure 1A, B)

Cassis schnireli Petuch, 1994 (Figure 1G, H)

Cassis viliusi Petuch and Berschauer, n. sp. (Figure 1C, D)

Tarantian Stage, Late Pleistocene: 126,000-17,700 ybp

Fort Thompson Formation, Coffee Mill Hammock Member

Cassis cf. *spinella* Clench, 1944

In addition to these large Pliocene and Pleistocene species, two small and rare *Cassis* taxa are also known from northern Florida and southern Georgia, and these include *Cassis*

flintensis Mansfield, 1940 (Flint River and Suwannee Formations; Rupelian Age, Oligocene) and *Cassis delta* Parker, 1948 (Chipola Formation; Burdigalian Age, Early Miocene). The four Calabrian-aged Holey Land species appear to be the direct ancestors of the four *Cassis* species that are now living in Florida and the tropical western Atlantic. These include: *Cassis madagascariensis* (Lamarck, 1822) (Florida Keys, Yucatan, and Caribbean Sea area only), which is the descendant of the Bermont *C. schnireli*; *Cassis spinella* Clench, 1944 (Cape Hatteras to the Florida Keys and the entire Gulf of Mexico), which is the descendant of the Bermont *S. viliusi*; *Cassis flammea* (Linnaeus, 1758) (Florida Keys and Caribbean Sea area only), which is the descendant of *C. rasae*; and *Cassis tuberosa* (Linnaeus, 1758) (Florida, Gulf of Mexico, Caribbean Sea, and south to Cabo Frio, Brazil), which is the descendant of *C. jameshoubrieki* (Figures 1E, F). Southeastern Florida, the Florida Keys, and the Yucatan Peninsula of Mexico are the only places where the northern (Carolinian Province) *C. spinella* occurs sympatrically with the southern (Caribbean Province) *C. madagascariensis*; north of Florida and Yucatan, only *C. spinella* occurs, while south of Florida and Yucatan, only *C. madagascariensis* can be found.

Although numerous tonnids of the genus *Malea* are known from the fossil beds of the Caribbean Region and South America, as well as the Eastern Pacific from California to Central America, the few records of the genus in the southeastern United States are known only from the fossil beds of southern Florida (Petuch, 1989; 1994; 2004). Only three *Malea* species are known from southern Florida, and these include the following (arranged here chronologically and stratigraphically and all illustrated on Figure 2):

Piacenzian Stage, Late Pliocene: 3.6-2.58 mya

Tamiami Formation, Fruitville Member

Malea hyaducki Petuch & Berschauer, n. sp. (Fig. 2A, B)

Gelasian Stage, Early Pleistocene: 2.58-1.8 mya

Caloosahatchee Formation, Fort Denaud Member

Malea springi Petuch, 1989 (Figure 2C, D)

Calabrian Stage, Early Pleistocene: 1.8 mya-780,000

Bermont Formation, Holey Land Member

Malea petiti Petuch, 1989 (Figure 2E, F)

ACKNOWLEDGMENTS

We thank the following individuals for their assistance in conducting field work and for their generous donation of type material: Edward Volek (Palm Beach Aggregates, Inc.), for helping with the collection of fossil helmet shells; Enrique Tomeu (owner of Palm Beach Aggregates, Inc.), for allowing the senior author access to collecting within his company's quarries; Harry Hyaduck, Sr. for helping with collecting in both the Rucks Pit and at Palm Beach Aggregates and for generously donating the holotype of the new *Malea*; Eddie Rucks (owner of the Rucks Pit), for allowing the senior author to collect in the Fort Drum quarries; and to Joseph Bucheck, Jr., Ernest ("Al") Klatt, Jr., Gary Leonard, Harry Yingst, Michael Bruggeman, Clifford Swearingen, Eddie Matchett, James Houbrick, Herbert and Fonda Waldron, Anthony Cinelli, Dr. Anton Oleinik, Phyllis Diegel, Richard Duerr, and Brian Schnirel, for helping the senior author collect helmet shells in the Palm Beach Aggregates quarries.

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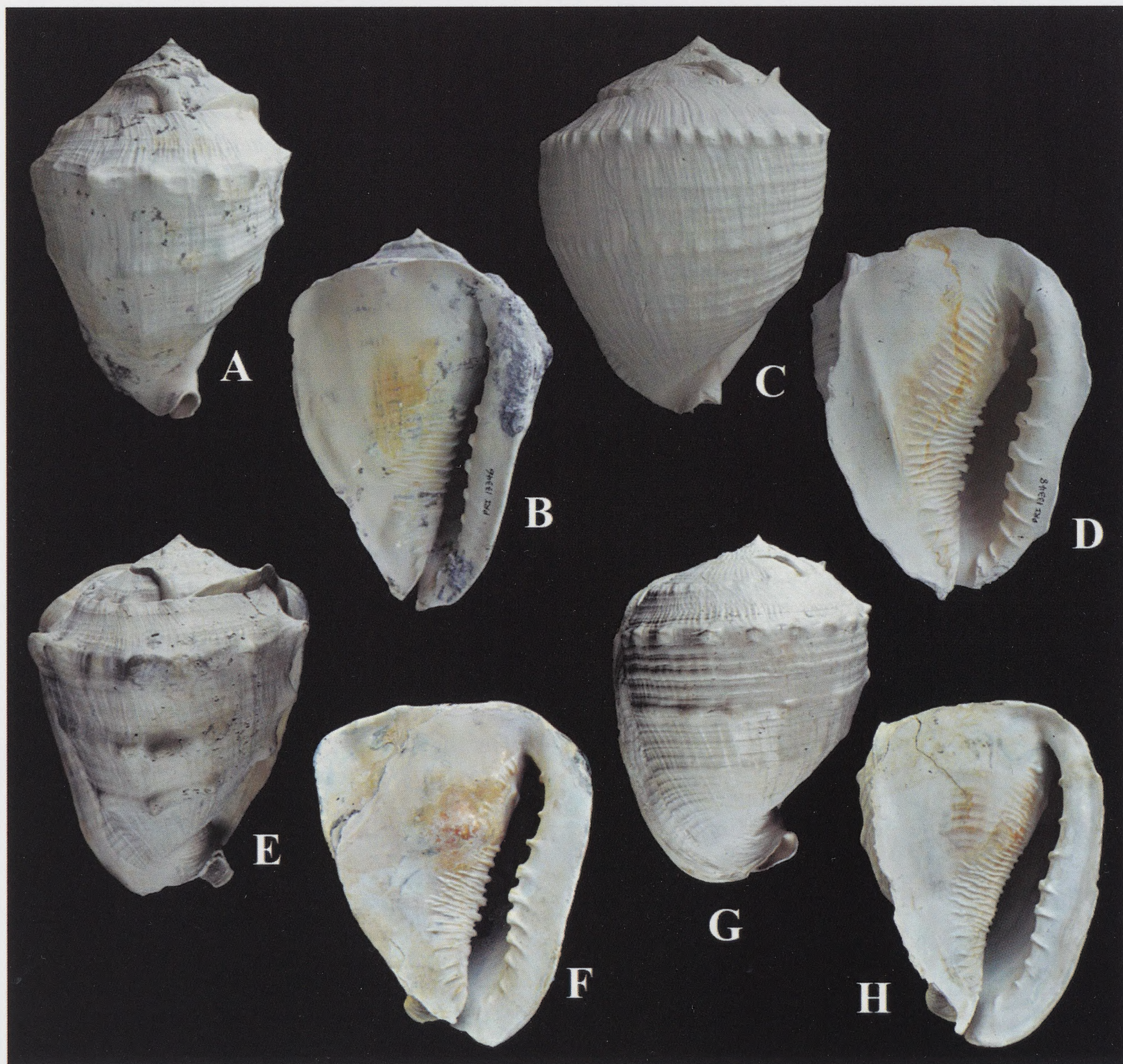


Figure 1. *Cassis* species from the Holey Land Member of the Bermont Formation (Calabrian Stage, Early Pleistocene).

A, B= *Cassis rasae* Petuch and Berschauer, new species, holotype, length 108.4 mm, PRI 13346; collected in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida; **C, D= *Cassis viliusi*** Petuch and Berschauer, new species, holotype, length 115.1 mm, PRI 13348; collected in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida; **E, F= *Cassis jameshoubrickii*** Petuch, 2004, length 203 mm, in the research collection of the senior author; collected in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida; **G, H= *Cassis schnireli*** Petuch, 1994, length 186 mm, in the research collection of the senior author; collected in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida.



Figure 2. *Malea* species from the Pliocene and Pleistocene of southern Florida.

A, B= *Malea hyaducki* Petuch and Berschauer, new species, holotype, length 120 mm, holotype, PRI 13349; collected in Rucks Pit, Fort Drum, Okeechobee County, Florida, from the Fruitville Member (Kissimmee River Valley equivalent) of the Tamiami Formation, late Piacenzian Stage, Late Pliocene; **C, D=** *Malea springi* Petuch, 1989, length 202 mm, in the research collection of the senior author; collected along the Miami Canal, 10 miles south of Lake Harbor, Palm Beach County, Florida; from the Fort Denaud Member of the Caloosahatchee Formation, Gelasian Stage of the Early Pleistocene; **E, F=** *Malea petiti* Petuch, 1989, length 122 mm, in the research collection of the senior author; collected in Palm Beach Aggregates Pit #6, Loxahatchee, Palm Beach County, Florida; Holey Land Member of the Bermont Formation, Calabrian Stage of the Early Pleistocene.

Description of two new cone species from Eastern Cape, South Africa, in the subgenus *Sciteconus*, Da Motta, 1981

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ABSTRACT The conid subgenus *Sciteconus* is re-visited and two new species, *Floraconus* (*Sciteconus*) *mosterti* and *F. (S.) markpagei* are described herein.

KEYWORDS Eastern Cape, *Floraconus*, *Sciteconus*, *mosterti*, *markpagei*, *bairstowi*, *nahoonensis*, *mpenjatiensis*

INTRODUCTION

The subgenus *Sciteconus* seems to have been introduced by Da Motta to focus on certain endemic South African cone species. Stephan Veldsman in 2016, using material and the guidance of the sharp eye of the late Arie Jooste, with addition of material by this author, worked on shells from the Eastern Cape that formed part of a so-called “*brianhayesi*” group. This group consists of small cones with distinctive nipple-like protoconch and convex spire whorls, found mainly at 90 -110 metres by dredging, of which he introduced four new species.

In terms of systematics, the author feels more comfortable with the logic of Puillandre *et al.* in 2014, in the Journal of Molluscan Studies, to maintain *Sciteconus* as a subgenus of *Floraconus*, removed from the eclectic group of species gathered recently under the umbrella of *Floraconus* by Monnier *et al.* 2018.

Including the two new species in this paper, a ‘string’ of related *Sciteconus* species, from southern Kwazulu-Natal to Port Alfred in the Eastern Cape (Capean Subprovince) is acknowledged. Nothing is yet known of their feeding habits and living specimens are virtually

unheard of, leaving DNA and radula type as a current mystery to entice future researchers.

ABBREVIATIONS

NMSA	KwaZulu-Natal Museum, Pietermaritzburg, South Africa
n. sp.	New species
pers. comm.	Personal communication

SYSTEMATICS

Superfamily Conoidea J. Fleming, 1822

Family Conidae J. Fleming, 1822

Genus *Floraconus* Iredale, 1930

Subgenus *Sciteconus* da Motta, 1991

Floraconus (*Sciteconus*) *mosterti* R. Aiken,
n. sp. (Figure 1, Plate 1)

Description. Shells fairly small, averaging 21.8 mm in size. Shape broadly conical, spire moderately depressed, suture indented, spire whorls convex with spaced axial dashes of colour. Protoconch nipple-like. Labrum curved, aperture narrow. Background colour white, overlaid with a pattern of relatively large nearly square brown blotches and thinner dashes,

forming an almost checker board pattern in some specimens. Base of shells purple-brown.



Figure 1. *Floraconus (Sciteconus) mosterti* R. Aiken, new species

Types.

Holotype: 22.2 x 12.6 mm. (Plate 1.1). NMSA P1450/T4410.

Paratype 1: 21.8 x 12.2 mm. R. Aiken Collection.

Paratype 2: 22.9 x 12.9 mm. R. Aiken Collection.

Paratype 3: 22.0 x 11.8 mm. R. Aiken Collection.

Paratype 4: 19.0 x 10.7 mm.
A. Seccombe Collection.

Paratype 5: 19.4 x 11.0 mm. R. Aiken Collection.

Paratype 6: 23.2 x 12.2 mm. R. Aiken Collection.

Paratype 7: 24.0 x 13.0 mm. M. Page Collection.

Distribution. Dredged off Port Alfred, Eastern Cape Province, South Africa at 90 to 115 metres.

Etymology. This species is named for its discoverer, Stephan 'Mossie' Mostert.

Discussion. Falling definitely morphologically and size wise into the '*brianhayesi*' group, this species, with its pale background and "checkered" pattern, bears no likeness to any of the seven *Sciteconus* species illustrated by Veldsman in *Malacologia* 92, pages 34 and 35.

Floraconus (Sciteconus) markpagei R. Aiken,
n. sp. (Figure 2, Plate 2)

Description. Shells small, averaging 21.4 mm in size, conical, spire low, suture mildly indented. Nipple-like protoconch, spire whorls faintly convex, shoulder rounded, spire marked with angled brown flecks, sometimes triangular. Background colour pale cream, overlaid with a series of brown markings of varying length, in 8 to 9 regularly broken radial bands. Base of shells tinged with plum colour.

Types.

Holotype: 20.8 x 11.3 mm. NMSA P1451/T4411.

Paratype 1: 24.2 x 13.7 mm. R. Aiken Collection.

Paratype 2: 22.0 x 12.1 mm. R. Aiken Collection.

Paratype 3: 19.0 x 11.3 mm. R. Aiken Collection.

Paratype 4: 19.1 x 10.8 mm. A. Seccombe Collection.

Paratype 5: 23.5 x 12.9 mm. M. Page Collection.



Figure 2. *Floraconus (Sciteconus) markpagei* R. Aiken, new species.

Distribution. Dredged at 100 metres between Port Alfred and Kenton-on-Sea, Eastern Cape Province, South Africa.

Etymology. This species is named for Mark Page, in gratitude for his research, suggestions, editing as well as photography of recent papers by the author.

DISCUSSION

To avoid confusion with other specific members of the subgenus *Sciteconus*, it is felt that a detailed account and presentation of comparable

species would be prudent at this juncture, due to their resemblance to the newly described species, as follows:

1) *Floraconus (Sciteconus) bairstowi* G. B. Sowerby III, 1889: Described from an Algoa Bay specimen in the Bairstow collection by Sowerby III in 1889, the type is way above average size at 51 mm. It was tracked and illustrated by Mike Filmer, and can be viewed on Gastropods.com (Hardy, 2020). Until the last decade, decent or live specimens were rare indeed. Ranging from 29 to 51 mm, the shells are robust, with different spire and broad aspect, and can be beach collected, alluding to a shallow water habitat. They exhibit most often a lovely pattern of dark brown somewhat large square shaped markings, that are set apart in a radial pattern on the whorl, usually in seven rows. Interestingly, there occurs a noticeable ‘form’ of this species, which has no ‘loose block’ pattern at all, and is replaced by light axial flames, sometimes even blending into a pale brown coloured mass on the whorl. A superb, fresh looking example of this variant can be seen as shell number 8, on page 488 of the recent Taxonomic Iconography of Living Cones. (Monnier *et al.* 2018) Further investigation into this variety is warranted. See Plate 3, Figure 1, for comparison. *F. (Sciteconus) markpagei* is a much smaller species, with different spire, morphology and whorl pattern. It is a deep-water species.

2) *Floraconus (Sciteconus) nahoonensis* (S. G. Veldsman, 2016): This species has remained enigmatic, having been described from a somewhat diverse group of specimens. A fortunate acquisition of an old collection rich in Eastern Cape material has provided some specimens that give a clearer picture of this species. These assumed beach shells are in fair condition and exhibit consistently, “species traits”, such as medium size (23.2 to 26.3 mm),

relatively sparse, spaced, smaller dorsal patterning, and morphologically not as “cone shaped” as the broader *bairstowi*. This species is however, larger than *markpagei*, has a more relatively small, spread pattern, and is morphologically more elongate.

3) *Floraconus* (*Sciteconus*) *mpenjatiensis* (Veldsman, 2016): This species also has dashes of brown in a radial pattern on the whorl, but can be separated from *markpagei* as follows: It is on average larger, and also broader, with more rounded, less conical profile. The broken radial pattern is thinner, (Plate 3 Figures 4 and 6c), in more close-set bands, sometimes with a different or non-existent zone below the centre of the whorl. The two species are separated by about 700 km of water.

4) Although rare, *Floraconus* (*Sciteconus*) *markpagei* has been displayed on the internet as an image in Wikipedia (as *bairstowi*), and the same image is repeated in Gastropods.com. This 19.6 mm specimen by ‘medvedev’ (Alexander Medvedev, of Moscow, Russia) is a fine example of *markpagei* with its small size, nipple-like protoconch and convex spire. It is highly dubious that the very large operculum came from that specimen though. See Plate 3 Figures 1-2 for a comparison between *F. (S.) bairstowi* and *F. (S.) markpagei*.

5) Of interest is the Alphabetical Revision of the species in recent Conidae, by Coomans, Moolenbeek & Wils in Basteria 46, 1982. Their three figures are: 194; *bairstowi* “flamed” form, 195; Sowerby’s drawing of the type, and 196: actually *F. (S.) nahoensis*.

6) In The Strandloper 225 of June 1989, Liltved and Millard produce a comprehensive article on the then-known *Conus* species of South Africa and on page 9 figure 18, illustrate a series of

“*bairstowi*”. In fact, their specimen on the lower left is another fine example of *markpagei*.

7) For the sake of comparison in this subgenus, see also in A Conchological Iconography of the Family Conidae in South Africa, on page 21, two superb examples of *F. (Sciteconus) velliesi*, with Holotype of *brianhayesi*, and on Plate 200, shells 1, 2, 5 & 6 are *F. (Sciteconus) "ariejoostei"* (Tenorio & Monteiro 2008).

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Plate 1. Figures: **1.** *Floraconus (Sciteconus) mosterti* n. sp. (22.2 x 12.6 mm) – Holotype; Port Alfred, Eastern Cape Province, South Africa; NMSA P1450/T4410. **2.** *Floraconus (Sciteconus) mosterti* n. sp. (21.8 x 12.2 mm) – Paratype 1; Port Alfred, Eastern Cape Province, South Africa; Aiken Collection. **3.** *Floraconus (Sciteconus) mosterti* n. sp. (22.9 x 12.9 mm) – Paratype 2; Port Alfred, Eastern Cape Province, South Africa; Aiken Collection. **4.** *Floraconus (Sciteconus) mosterti* n. sp. (19.0 x 10.7 mm.) – Paratype 4; Port Alfred, Eastern Cape Province, South Africa; Seccombe Collection. **5.** *Floraconus (Sciteconus) mosterti* n. sp. (23.2 x 12.2 mm) – Paratype 6; Port Alfred, Eastern Cape Province, South Africa; Aiken Collection. **6.** *Floraconus (Sciteconus) mosterti* n. sp. (22.0 x 11.8 mm) – Paratype 3; Port Alfred, Eastern Cape Province, South Africa; Aiken collection.



Plate 2. Figures: **1.** *Floraconus (Sciteconus) markpagei* n. sp. (20.8 x 11.3 mm) – Holotype; Eastern Cape Province, South Africa; NMSA P1451/T4411. **2.** *Floraconus (Sciteconus) markpagei* n. sp. (24.2 x 13.7 mm) – Paratype 1; Eastern Cape Province, South Africa; R. Aiken Collection. **3.** *Floraconus (Sciteconus) markpagei* n. sp. (22.0 x 12.1 mm) – Paratype 2; Eastern Cape Province, South Africa; Aiken Collection. **4.** *Floraconus (Sciteconus) markpagei* n. sp. (19.0 x 11.3 mm) – Paratype 3; Eastern Cape Province, South Africa; Seccombe Collection. **5.** *Floraconus (Sciteconus) markpagei* n. sp. (19.1 x 10.8 mm) – Paratype 4; Eastern Cape Province, South Africa; Seccombe Collection. **6.** *Floraconus (Sciteconus) markpagei* n. sp. (23.5 x 12.9 mm) – Paratype 5; Eastern Cape Province, South Africa; Page Collection.

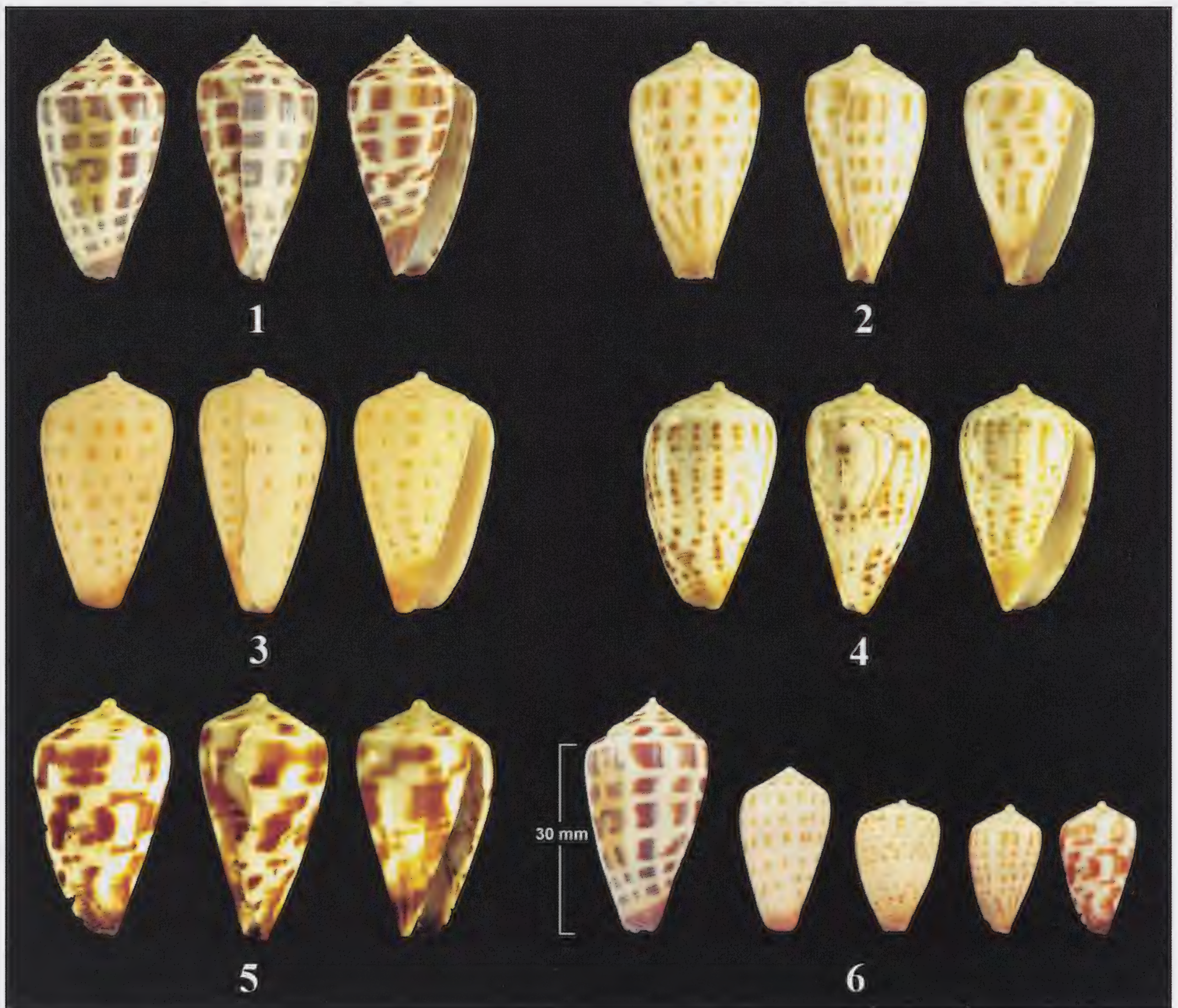


Plate 3. Figures: **1.** *Floraconus (Sciteconus) bairstowi* G.B. Sowerby III, 1889 (37.9 x 20.0 mm); Eastern Cape Province, South Africa; Aiken Collection. **2.** *Floraconus (Sciteconus) markpagei* n. sp. (20.8 x 11.3 mm) – Holotype; Eastern Cape Province, South Africa; NMSA P1451/T4411. **3.** *Floraconus (Sciteconus) nahoonensis* (S. G. Veldsman, 2016) (24.6 x 13.9 mm); Southern Kwazulu-Natal, South Africa; Aiken Collection. **4.** *Floraconus (Sciteconus) mpenjatiensis* (S. G. Veldsman, 2016) (21.5 x 13.8 mm) - Paratype 2; Southern Kwazulu-Natal, South Africa; Aiken Collection. **5.** *Floraconus (Sciteconus) mosterti* n. sp. (21.8 x 12.2 mm) – Paratype 1; Port Alfred, Eastern Cape Province, South Africa; Aiken Collection. **6.** From left to right: *Floraconus (Sciteconus) bairstowi* G.B. Sowerby III, 1889, *Floraconus (Sciteconus) nahoonensis* (S. G. Veldsman, 2016), *Floraconus (Sciteconus) mpenjatiensis* (S. G. Veldsman, 2016), *Floraconus (Sciteconus) markpagei* n. sp., and *Floraconus (Sciteconus) mosterti* n. sp.

Large Eastern Cuban Slugs: Overview of an Enigmatic and Forgotten Group

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ABSTRACT New findings of larger slugs from different localities of eastern Cuba, belonging to the family Veronicellidae (Gray, 1840), are revealed. Three of these species could be new to science. This paper verifies the geographic distribution, color forms and sizes, based on the evidence known to date.

KEY WORDS Cuban slugs, *Veronicella*, *Veronicella tenax*

INTRODUCTION

Cuban slugs are not the most exciting of the archipelago land molluscs and have received little or no attention since the earlier malacology works. The genus *Veronicella* (Blainville, 1817) is currently represented by only three species [*Veronicella cubense* (Pfeiffer, 1840); *V. sloanei* (Cuvier, 1817); and *V. tenax* (Baker, 1931)] There are two other slugs known to occur on other Caribbean islands and part of the American continent mainland [*Leidyula floridana* (Leidy & Binney in Binney, 1851); *Sarasinula plebeia* (Fisher, 1868)]. Here we exclude the species reported for the Genus *Deroceras* (Rafinesque, 1820) [Limacidae]. Of all these species, only *V. tenax* is endemic to Cuba and noticeable for its larger size and color patterns.

In the late 1940's, Carlos Guillermo Aguayo and Miguel Luis Jaume acknowledged a new species of *Veronicella* from the Pico de Turquino vicinity without formally introducing the taxon (Aguayo & Jaume, 1947-1951;

Maceira, 2003). Thanks to the Nipe-Sagua-Baracoa Massif project, David Maceira, a local malacologist, began collecting large slugs from some of these localities in 1998 (e.g., Yumurí-Maisí plateau) (R. Teruel, personal communication). In 2002, a group of researchers published their work on the diversity of the Sierra de Cristal province (Fa, *et al.*, 2002. p. 5) noting that one of the *Veronicella* sp. was considered endemic from 3 localities in the montane forest.

In 2003, Maceira examined the species of the family Veronicellidae from Cuba but limited his work to a bibliographic revision. A couple of years later, the same author (Maceira, D. *et al.*, 2005. page 61), in a Rapid Biological Inventories Report about La Bayamesa National Park area, reported: “in the ground molluscs fauna, I found a terrestrial slug, *Veronicella* sp. nov., which is a new species for science and the sole representative of the *Gymnomorpha* subclass in the mountain rain forest”. He found this species under stones and leaf litter and concluded that it was an uncommon taxon from

Sierra Maestra Massif. In another similar report published the same year related to the Alexander of Humboldt National Park biodiversity, Maceira mentions another new local endemic *Veronicella* species “*living under rocks*” in all sectors of the park (Fong, A. *et al.*, 2005. pp. 82 and 319). In a general study of the mountain rainforests molluscan fauna of Cuba, this author added 2 new localities, Pico Bayamesa and El Zapato, for this new species (Maceira & Lauranzón, 2008). Unfortunately, these species were not described.

At the same time, on a field trip to Yunque de Baracoa peak in 2003, Adrián González-Guillén identified a new large specie of slug, blackish in color inhabiting that peak (González-Guillén, A. 2008. p. 64). This new species had not been previously reported from this location; an area where land snails collecting has been taking place since the late 19th century. About a year later a few pictures and references to unidentified eastern slugs appeared in a book on Cuban land snails, but without providing locality information (Espinosa & Ortea, 2009). More recently and since 2010, malacologists, zoologists, naturalists and even tourists have begun finding and recording larger slugs from Eastern Cuba (*i.e.*, Pico Turquino area, Sierra de Cristal, Yumurí, etc.).

One interesting publication (Fernández-Velázquez, *et al.*, 2015. p. 69) about the Moa region biodiversity briefly mentions a new *Veronicella* species from Farallones de Moa, but nothing more. Regrettably and until today, even with all the relevant collecting from the last 20 years, nothing has been published about these new *Veronicella* species, their taxonomy or ecology.

The external morphology of veronicellids, and slugs in general, is insufficient for taxonomical purposes. However, the variability in Cuba, as

well as the unique and remote places where some specimens have been recorded (*e.g.*, high altitude rainforests and remote isolated karstic hills), provide sufficient clues in the search for potential new species, which constitutes the main aim of our work.

Such reports are frequent and in some cases well illustrated but with localities omissions or vice versa. Some specimens of new species formerly registered reside in zoological collections that are, in most cases, unobtainable, and there are other inconsistencies as mentioned above. All these factors tend to fundamentally diminish any conservation efforts in these fragmented areas.

MATERIALS AND METHODS

Here we have assembled all the findings of Eastern large slugs together with our knowledge of Western Guaniguanico mountain range slugs. All the specimens photographed and shown in this paper were not collected. However, previous material collected by David Maceira, Abelardo A. Méndez-Hernández and Luis A. Lajonchere confirmed our records. Collected specimens are placed in the malacology collection of the Zoology Department at Centro Oriental de Ecosistemas y Biodiversidad in Santiago de Cuba. Size measurements were taken when the animals were crawling naturally or motionless *in situ*.

DISCUSSION

The following taxa are what we consider large slug species endemic to Cuba:

Veronicella tenax (Baker, 1931). Type locality: Cueva de Tiburón, Ensenada de San Vicente, Pinar del Río province. Distribution: Guaniguanico mountain range, from San Cristóbal river west side in Sierra del Rosario to

the southern end of Sierra de Guane in Sierra de Los Órganos, Pinar del Río province [see map 1]. Approximate size: 13-16 cm. Common name: Lengua de vaca (cow's tongue). Coloration: light to mustard yellow, cream to orange, beige, brownish, gray-green, light gray and lead gray. The slugs can have no markings or display dark black to light gray spotting [Plate 2, Figures 18-19; Plate 3, Figures 20-25]. Remarks: Some of us considered that specimens found in the areas encompassed by Taco-Taco and San Cristóbal rivers could be subspecies of *V. tenax* [Plate 2, Figures 13-17].

***Veronicella* sp. #1.** Distribution: Aguada de Joaquín [Plate 1, Figure 4], and "Paso de los Monos" [Plate 1, Figure 5], in Pico Turquino, Santiago de Cuba province ('Monkeys Path' locality is 300 meters up from the other locality, see Map 2.1) as well as Pico La Bayamesa and El Zapato, both from Granma province (see Map 2.2. Approximate size: 10-13 cm. Coloration: light to very dark gray background with small whitish dots more dense along the perimeter edge and a white dorsal line.

***Veronicella* sp. #2.** Distribution: La Tabla [Plate 1, Figures 1-3] (See Map 2.3) and neighboring localities, Carso de Baire, Segundo Frente municipality, Santiago de Cuba province. Approximate size: 10-11 cm. Coloration: gray-white, dark gray almost black bordered. These slugs exhibit irregular white and dark gray markings.

***Veronicella* sp. #3.** Distribution: Based on our findings, this species appears to inhabit 2 wider areas, the Maisí Plateau and Alturas de Baracoa, Guantánamo province at various localities listed below:

- **Locality:** El Beril, southwest Maisí upper marine terrace, Maisí municipality (see Map 2.4). Approximate size: 8-10 cm. Coloration:

the top of the animal is brownish to almost black with bright yellow foot underneath [Plate 2, Figure 12].

- **Locality:** Cañón de Yumurí (river canyon), Maisí and Baracoa municipalities (see Map 2.5). Approximate size: 10-13 cm. Coloration: Brown or black specimens have foot border mottled in bright yellow, beige or white. Other specimens almost white leaving only an irregular dark dorsal band. All showing bright yellow foot underneath [Plate 1, Figures 6-7].

- **Locality:** "Curva de los mancaperos" and other Yunque de Baracoa hill areas, Baracoa municipality (see Map 2.6). Approximate size: 10-15 cm. (larger size R. Teruel, personal communication). Coloration: Dark brown or black specimens with a yellow thin borderline. All showing bright yellow foot underneath [Plate 1, Figures 8-11].

- **Locality:** Duaba river vicinity, Baracoa municipality. Approximate size: 10-12 cm. Coloration: gray-yellow mustard background predominantly with yellowish or darker gradations of such pattern. Narrow dorsal band and foot borderline reinforced with gray-brownish.

- **Locality:** Taco vicinity, Baracoa municipality. Note: We were unable to obtain pictures from this locality population for this paper in order to describe its color deviations.

Remarks: The blackish pigmentation in these slugs is not as pure or deep as we often see in the adult European species *Arion ater* (Linnaeus, 1758), but could be similar to the velvet black coloring of American slug *Belocaulus angustipes* (Heynemann, 1885). Curiously, Maceira (2005) mentions the presence of these large slugs in all areas of Humboldt National Park.

***Veronicella* sp. #4.** Distribution: Sierra de Cristal, Holguín and Santiago de Cuba provinces (see Map 2.7). Approximate size: 10-

11 cm. Coloration: Uniform opaque brown-chestnut or brown-yellow mustard bordered in gray. These slugs may have no marking or display irregular dorsal spotting. Remarks: These slugs were collected and sighted in Levisa river east side (*i.e.* Cuesta de Seboruco in Farallones de la Italiana) and Arroyo Manzano [Plate 3, Figure 26], Miguel river affluent, in Santiago de Cuba province side.

Phyllocaulis species are large South American veronicellids that can reach or surpass 10 cm in length [*e.g.* *P. gayi* (Fisher, 1871), *P. boraceicensis* (Thomé, 1972) and *P. tuberculosus* (E.von Martens, 1868)]. However, large land slugs may reach 15 cm or more. Some of the world's largest well-known slugs are the colorful east Australian *Triboniophorus graeffei* (Humbert, A. 1863) and European black slug *Arion ater* (Linnaeus, 1758). These slugs can reach up to 18-20 cm. Other large species include the European leopard slug *Limax maximus* (Linnaeus, 1758) and some North America Pacific northwest banana slugs species from *Ariolimax* (Mörch, 1859) [*A. dolichophallus* (Mead, 1943) and *A. californicus* (Cooper, 1872)]. There are species like *Ariolimax columbianus* (Gould, 1851), that reach 25 cm. The European keel back slug *Limax cinereo-niger* (Wolf, 1803), can reach 30 cm. and is considered the largest land slug on Earth.

The largest Cuban slugs are *V. tenax* from the Sierra de los Orgasno range. Undoubtedly, in the west, the The largest specimens of *V. tenax* are spotted populations that come from the west Sierra de los Órganos range. Further, the largest specimens of the eastern region could be those found at Yunque de Baracoa peak (*Veronicella* sp. #3). When crawling and stretching over rocks these slugs are able to enlarge their size considerably.

CONCLUSIONS

New findings of larger slugs which apparently to belong to Veronicellidae (Gray, 1840) have been reported since the early 21st century from different localities in eastern Cuba [see maps]. There could be at least 3 new species. Populations from the Turquino and Bayamesa peaks vicinity and Baire Karst could be related to one another. These eastern new species relict populations are mainly living in karstic areas associated to distant mountain and cloud rainforests, which are evidence of of complex evolutionary processes throughout the last 25-20K years.

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Map 1. Cordillera de Guaniguanico



Map 2. Various localities. 1= Aguada de Joaquín and Paso de los Monos, Macizo del Turquino, Sierra Maestra; 2= El Zapato and Pico La Bayamesa, Sierra Maestra; 3= La Tabla, Carso de Baire; 4= El Beril, Meseta de Maisí; 5= Canon del río Yumurí, límite Baracoa-Maisí; 6= Yunque de Baracoa-Duaba, Baracoa; 7= Este del río Levisa and Arroyo Manzano, Sierra de Cristal.



Plate 1. *Veronicella* sp., 1-3: La Tabla and neighboring localities, Carso de Baire, Segundo Frente municipality, 4: Aguada de Joaquin, Pico Turquino, Santiago de Cuba Province, 5: Paso de los Monos, Pico Turquino, Santiago de Cuba Province, 6-7: Cañón de Yumuri, Maisí and Baracoa municipalities, 8-11: Curva de los Mancaperros and other Yunque de Baracoa hills area, Baracoa municipalities.



Plate 2. *Veronicella* sp., 12: El Beril, southwest Maisí upper marine terrace, Maisí municipality, 13-17: Taco-Taco and San Cristóbal rivers, 18-19: *V. tenax* Cueva de Tiburón Ensenada de San Vicente, Pinar del Rio province.

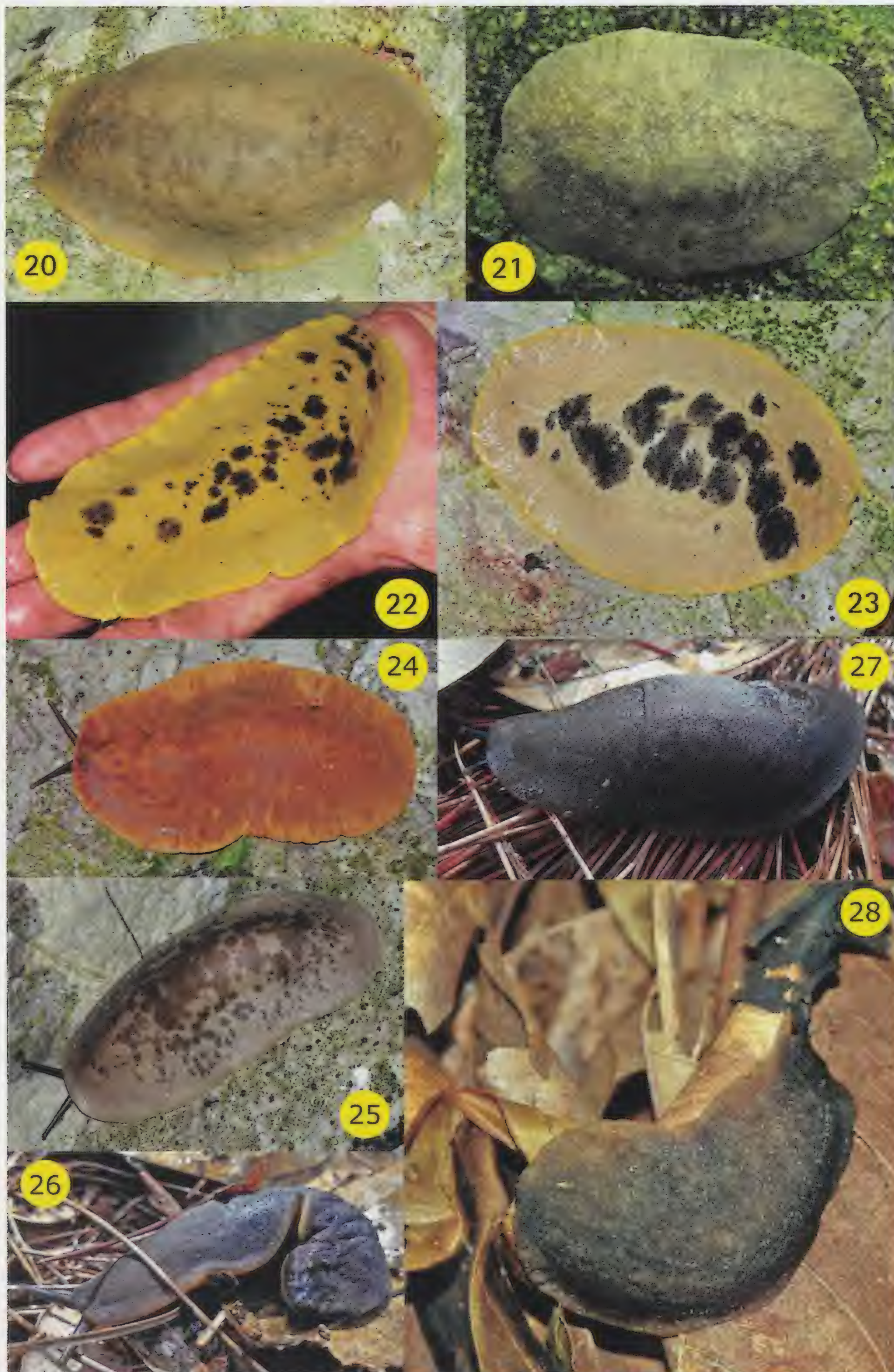


Plate 3. *Veronicella* sp., 20-25: *V. tenax*, Cueva de Tiburon, Ensenada de San Vicente, Pinar del Rio province, 26: Sierra de Cristal, Holquin and Santiago de Cuba provinces, 27-28: west Sierra de los Órganos range.

Resolving phylogenetic and classical nomenclature: A Revision of *Canarium* Schumacher, 1817 (Mollusca, Neostromboidae, Strombidae)

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ABSTRACT This revision of the genus *Canarium* Schumacher, 1817 after Abbott (1960) advances our understanding of the phylogeny of Strombidae. Morphological characters were used to generate a phylogeny using maximum likelihood and including all of the recognised species. This resulted in the recognition of one tree, and within that tree the existing genera *Canarium* Schumacher, 1817 *Tridentarius* Kronenberg & Vermeij, 2002 and *Terestrombus* Kronenberg & Vermeij, 2002, and two more *Maculastrombus* n. gen. and *Neostrombus* n. gen. were recognisable clades. Furthermore, within the genus *Canarium*, four subgenera, *Canarium* (*Canarium*), *Canarium* (*Conundrum*), *Canarium* (*Elegantum*), and *Canarium* (*Stereostrombus*), were identified and described. We describe and define taxa that are compatible with the requirements of the International Code of Phylogenetic Nomenclature (PhyloCode 2020), and also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). This revision assists in generating a system of nomenclature that reflects the hypothetical relationships, and is at the same time practical in its application. We designate type localities and types for included species that were not yet addressed up until now.

KEY WORDS *Canarium*, *Conundrum*, *Elegantum*, ICZN, *Maculastrombus*, *Neostrombus* PhyloCode, *Stereostrombus*, Taxonomy

INTRODUCTION

The start of this decade has seen a flourish of work on the Stromboidae (Maxwell *et al.* 2020a; Dekkers 2020; Dekkers and Maxwell 2020a; Liverani *et al.* 2021). Consequently, there has been a significant shift in the understanding of the relationships between taxa, and this has commenced to be reflected in the nomenclature (Maxwell *et al.* 2020a; Dekkers and Maxwell 2020a). We use the International Code of Phylogenetic Nomenclature (PhyloCode 2020), and demonstrate how its application can also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999).

Abbott (1960) viewed the *Canarium* Schumacher, 1817 as a large subgenus of Indo-Pacific Strombidae incorporating the smaller species of the family that were generally compact shape, with unflaring lips, lirate mouths and strombid operculum not curved. Abbott (1960) presented the fossils for the “*urceus-mutabilis-labiatus* Group” representing a taxonomic demarcation to gather the preceding taxa into a collective group, before presenting the remaining taxa. Many of these remaining taxa have now been removed from *Canarium* into genera such as *Terestrombus* Kronenberg & Vermeij, 2002 and *Tridentarius* Kronenberg & Vermeij, 2002, while others such as the *Canarium elegans* complex remain still

taxonomically nested in the “*urceus-mutabilis-labiatus* Group”.

We present a revision of the *Canarium* as defined by Abbott (1960), and provide a hypothesis for the relationships between species in that taxa which is then reflected in the nomenclature. We erect taxa providing a definition, diagnosis and description (Benton 2000; Maxwell *et al.* 2020a) in compliance with both the ICZN (1999) and PhyloCode (2020), bringing an evolutionary contextualisation of the nomenclature with the *Canarium* clade. Demonstrating that the goals of the PhyloCode, and the ICZN requirements for validity within the nomenclature are not mutually exclusive.

Abbreviations

AMNH	American Museum of Natural History, New York, USA.
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, USA
IRNSB	Institut Royal des Sciences Naturelles, Brussels, Belgium.
MHG	Muséum d'Histoire de Genève, Geneva, Switzerland.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMUK	Natural History Museum United Kingdom, London, Great Britain.
QM	Queensland Museum, Brisbane, Australia.
RMNH	Rijksmuseum voor Natuur Historie (now in Naturalis Biodiversity Center), Leiden, The Netherlands.
UZM	Museum of Evolution of Uppsala University, Uppsala, Sweden.
ZMA	Zoölogisch Museum Amsterdam (now in Naturalis Biodiversity Center), Leiden, The Netherlands.

METHODS

A total of 31 taxa were selected based on the classification of Abbott (1960) and the species included in that work or described later but within the subgenus *Canarium* (Table 1) or its derivatives. The (sub)genus *Canarium* of Abbott (1960) is at present regarded as sitting at the rank of genus (MolluscaBase eds. 2020).

Twelve characteristics were chosen for the discrimination of species morphological relationships; the coding is based on the type and examples from the type location (Table 1). Atypical (freak) examples of all species are known and have been omitted for character clarity. Characteristics can be grouped into five categories: 1) shape of shell (Characteristics A-C); 2) form of the labrum (Characteristics D-F); 3) form of columella (Characteristics G-I); 4) inner aperture (Characteristics J); and 5) morphology of the shell (Characteristics K-N).

The MEGA X (Kumar *et al.* 2018) software was used to determine morphologically based clusters of species. The use of software developed for molecular analysis of character states was tested and validated in previous studies with congruence when comparing new outputs with prior studies (Maxwell *et al.* 2020a). Trees were generated using Maximum Likelihood with a neutral evolutionary neutrality. Character states were transcribed and coded (1 = A, 2 = G, 3 = C, 4 = T) to represent states. Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor Markov 4 -state model (Jukes and Cantor 1969). All trees generated were tested using 50 bootstrap replications, which is reflective of the data matrix size. The principles and criteria for selection of natural clades for formal recognition were based on the theory of Benton (2000) after Maxwell *et al.* (2020a) and applied in Dekkers and Maxwell (2020a), with the

treatment of subspecies and species based on Maxwell and Dekkers (2019). A second data set, with weighting for characters C and D were conducted.

RESULTS

The unweighted character analysis using maximum likelihood analysis produced one tree with log likelihood of -225.20. One species, *Canarium* (*Conundrum*) *klineorum* (Abbott, 1960), was problematic in its placement in the characteristic generated tree because of distinctive cross-sectional labrum forms (Characteristics D and E). These distinctive characteristics are reflective of divergent evolutionary trajectories in form, and that a species complex has a fixed morphospace in form represented by these characteristics that binds them (Maxwell *et al.* 2020b). Given the hypothesised defining characteristic in lip rim, *Canarium klineorum* was placed at the base of the subgenus *Canarium* (*Conundrum*) n. subgen., this hypothesis of the relationships has been used and illustrated (Figure 1). This in practical terms, giving a greater explanatory weight to characteristic E.

Notwithstanding the approach herein, Bandel (2007) recognised that there was a collection of three genera that fell outside the *Canarium* genus, and the results support this hypothesis, and these have previously been recognised at the generic level as *Terestrombus* Kronenberg & Vermeij, 2002, *Tridentarius* Kronenberg & Vermeij, 2002, and *Neostrombus* n. gen. To this we add *Maculastrombus* n. gen. based on the form of the outer lip.

We herein identify four taxa that reflect natural groups with the genus *Canarium* Schumacher, 1817: *Canarium* (*Canarium*), *Canarium* (*Conundrum*) n. subgen., *Canarium* (*Elegantum*) n. subgen., and *Canarium* (*Stereostrombus*) n.

subgen.. The internal relationships between these subgenera may shift as more work is carried out, as such we have refrained from erecting formal ranks within the genus *Canarium*.

SYSTEMATICS

Phylum: Mollusca Linnaeus, 1758

Order: Sorbeoconcha Ponder & Lindberg, 1997

Superfamily: Stromboidea Rafinesque, 1815

Epifamily: Neostromboidae Maxwell, Dekkers, Rymer & Congdon, 2019

Family: Strombidae Rafinesque, 1815

Neostrombini Liverani, Dekkers & Maxwell, new tribe

Type Genus. We designate *Neostrombus* Liverani, Dekkers & Maxwell, new genus (Type: *Strombus fusiformis* Sowerby II, 1842).

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Canarium* Schumacher, 1817, *Maculastrombus* n. gen., *Neostrombus* n. gen., *Tridentarius* Kronenberg and Vermeij, 2002 and *Terestrombus* Kronenberg and Vermeij, 2002 and taxa more closely related to them than other members of Strombidae Rafinesque, 1815.

Diagnosis. Shells are small without a flaring lip, and a basal peg on the lateral teeth of the radula.

Description. Shells small with a narrow aperture that is posteriorly constricted forming a narrow sinus with the body whorl. The radula has a central tooth with five cusps the central being the largest, and lateral teeth with a basal peg.

Etymology. The name is formed from the combination of the genus *Neostrombus*, as “Neo+strombus+” where the prefix “Neo+” is also used to denote a crown clade, and the tribe suffix “+ini” to reflect the taxon’s position within the nomenclature.

Remarks. *Neostrombini* n. tribe differs from other Stromboidean tribes in being small and having non-flaring lip which is thickened toward the margin. The clade shares similarities in radula formulation with members of *Conomurex* Fischer, 1884 and Dolomenini Dekkers and Maxwell 2020a, in having a first lateral tooth with a basal peg.

Canarium Schumacher, 1817

Type Species. *Canarium ustulatum* Schumacher, 1817 (= *Strombus urceus* Linnaeus, 1758).

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus urceus* Linnaeus, 1758 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Diagnosis. Small solid shells with an elliptic-rhomboid form and a variable height of teleoconch, and a cross section of the labrum that is thickened with a fine ridge.

Original Description. “*Testa suboblonga; spira subelongata, acutiuscula. Apertura linearis, postice integerrima, coarctata; rostrum breve subadscendens, subrecurvum; canalis apertus; labium externum acutum, in dorso marginatum, antice lobo semilunari inter sinum sigmoideum et truncaturam obliquam, postice integerrimum, interne substriatum; labium internum callosum, adnatum, columellaque tortilli antice substriatum*” (Schumacher, 1817, p. 219). [Translation: Shell oblong; spire elevated, pointed. Aperture linear, complete in the back and narrowed; siphonal canal short, a bit abaperturally bent; canal open; external lip thickened, with sharp border, anteriorly have a semilunar lobe between the sinus and the oblique cut of the canal, in the back complete, internally slightly striated; internal lip callused, adherent, columella twisted and anteriorly a bit striated]. Note: both the original description and the translation need some interpretation: the

“*apertura postice integerrima*” means probably that the posterior canal is absent; this character is repeated in “*labium externum...postice integerrimum*”.

Canarium (Canarium) Schumacher, 1817

Type Species. *Canarium ustulatum* Schumacher, 1817 (= *Strombus urceus* Linnaeus 1758).

Diagnosis. The labrum cross section is spatulate in form and has a distinctive fine ridge centrally.

Description. A solid shell with an elliptic-rhomboid form and a variable height of teleoconch. The coloured columella is well formed over the length of the aperture, but lirations vary from the entire length to only anteriorly and posteriorly. The sculpture of the spire varies from smooth to highly ornamented.

Synonymy.

Canarium Schumacher, 1817, p. 219 (Type: *Canarium ustulatum* Schumacher, 1817 = *Strombus urceus* Linnaeus, 1758).

Strombidea Swainson, 1840, p. 138 (Type: *Strombus urceus* Linnaeus, 1758).

Conarium Jousseume, 1888, p. 174 (Type: *Strombus mutabilis* Swainson, 1821)

Conorium “Jousseume” Abbott, 1960, p. 63 (Printing error for *Conarium* Jousseume, 1888).

After much debating, the present authors are in agreement to synonymise the genera names *Conarium* Jousseume, 1888, and *Conorium* Abbott, 1960 with the genus *Canarium* Schumacher, 1817. Liverani *et al.* (2021) considered the genus name *Conarium* Jousseume an error for *Canarium*. In the previous entry on the same page, *Gibberulus gibberulus* (Jousseume, 1888, p. 174), Jousseume explicitly states: “Cette espèce ne pouvant être inscrite dans aucune des divisions connues, nous créons pour elle le genre

Gibberulus.” (being not possible to assign this species to any of the known divisions, we create for her the new genus *Gibberulus*). Such a statement is absent in the entry to *Conarium mutabilis*, making it probable that the different vocal is only a typographical refuse. *Conorium* (Abbott 1960) is a misspelling of *Conarium* Jousseume and, therefore, a misspelling of *Canarium* Schumacher, 1817. Abbott (1960) very probably wanted to synonymise the name *Conarium* Jousseume with the genus *Canarium* Schumacher, but on his turn made one more spelling error. We do not consider the reference to *Strombus mutabilis* Sow. (Sow., Th. Conch. Pl. VII, fig. 40, 45-47, 49-52) made by Jousseume as a fixation of type species, or as description, but purely as reference to the original first publication of the species, similar references have been made for all other species cited in Jousseume, 1888.

Included Taxa.

Strombus urceus Linnaeus, 1758, 745, no. 440 (Lectotype: UZM 685; Type Location: Singapore, designated by Maxwell *et al.* 2020c).

Lambis labiata Röding, 1798, p. 63, no. 806 (Holotype: Martini (1777), pl. 78, figs. 804 & 803; Type Locality: Amboina, Indonesia, designated by Abbott (1960), Röding (1798) gave no type locality.)

Strombus incisus Wood, 1828, p. 14, pl. 4, fig. 12 (Lectotype: Wood (1828) p. 14 pl. 4 fig. 12; Type Location: Labuan Bujo, Benonko Beach, Flores, Indonesia, designated by Maxwell *et al.* 2020d).

Strombus anatellus Duclos, 1844, pl. 4, figs. 11 & 12, and pl. 21, figs 8 & 9 (set of 3 syntypes: MNHN IM-2000-32467; Type Location: The Kangean Islands, Indonesia, designated by Maxwell *et al.* 2020d).

Strombus olydius Duclos, 1844, p. 4, pl. 5, fig. 7 (type: the type is presumably in MHG (fide Abbott 1960, p. 69); Type

Locality: Nossi-bé, northwest Madagascar, designated by Abbott 1960).

Strombus (Canarium) urceus orrae Abbott, 1960, p. 66, pl. 20, fig. 28, and pl. 41 fig. 5 (Holotype: ANSP 247756; Type Location: Augustus Island, Western Australia, designated by Abbott 1960).

Canarium esculentum Maxwell, Rymer, Congdon and Dekkers 2020c, p. 339, fig. 4 & 5 (Holotype: AMNH 12927; Type Location: Olango Island, Philippines, designated by Maxwell *et al.* 2020d).

Canarium daveyi Dekkers and Maxwell, 2020b, p. 346, fig. 1 (Holotype: RMNH MOL.112282a; Type Locality: Paulau Auri, Geelvink Bay, Indonesia, designated by Dekkers and Maxwell 2020b).

Canarium geelvinkbaaiense Dekkers and Maxwell, 2020b, p. 349, fig. 2 (Holotype: RMNH MOL.179571a; Type Locality: Manokwari, Western New Guinea, Indonesia, designated by Dekkers and Maxwell 2020b).

Canarium manintveldi Dekkers and Maxwell, 2020b, p. 351, fig. 3 (Holotype: ZMA MOLL.187523a; Type Locality: Malapoa Island, Vanuatu, designated by Dekkers and Maxwell 2020b).

Canarium youngorum Dekkers and Maxwell, 2020b, p. 354, fig. 4 (Holotype: QM MO.85756; Type Locality: Manus Island, Papua New Guinea, designated by Dekkers and Maxwell 2020b).

Canarium (Conundrum) Liverani, Dekkers & Maxwell, new subgenus

Type Species. *Strombus mutabilis* Swainson, 1821.

Diagnosis. A solid shell with a spathulate cross section of the outer lip with a fine ridge located on the inner edge.

Description. The solid shell is elliptic-rhomboid in form with a variable height of spire,

generally low. The cross section of the labrum is spatulate with a fine ridge located on the inner edge. The columella is well formed the length of the aperture and variable in liration from entirely lirate to being lirate posteriorly and anteriorly. The liration of the aperture is variable form distinct to obsolete. The mid teleoconch with distinct sculpture of tubercles which may form axial plications. The ventral body whorl is smooth.

Etymology. From the Latin “conundrum” in the neuter nominative singular, meaning enigma, caused by the long debate about the state of the name *Conarium* Jousseaume, 1888.

Included Taxa.

Strombus mutabilis Swainson, 1821, pl. 71
(The whereabouts of the Swainson physical type of *mutabilis* is unknown (Abbott 1960, p. 74); Type Locality: Cebu City, Cebu Island, Philippines (restricted by Abbott 1960, originally “East Indies”).

Strombus ostergaardi Pilsbry, 1921, p. 320, pl. 12 (Holotype: ANSP 74549; Type Locality: from the dredger dump on the harbour side of Sand Island, Honolulu, Pleistocene, designated by Pilsbry, 1921).

Canarium microurceum Kira, 1959, p. 37, pl. 15, fig. 5 (Holotype: the type figured by Kira 1959 is probably in the collection of Mr. Tetuaki Kira, Japan (fide Abbott 1960, p. 72); Type Locality: Shirahama, Honshu Island, Japan (restricted by Abbott 1960 from a broad range given by Kira)).

Strombus (Canarium) mutabilis ochroglottis Abbott, 1960, p. 74, pl. 20, figs. 9 & 10 (Holotype: ANSP 250187; Type Locality: Mauritius, designated by Abbott 1960).

Strombus (Canarium) klineorum Abbott, 1960, p. 70, pl. 20, figs. 20 & 21 (Holotype: ANSP 247621; Type Locality: Powder Bay, Trincomalee, Sri Lanka, designated by Abbott 1960).

Strombus (Canarium) wilsoni Abbott, 1967, p. 455, pl. 328, figs. 1 to 3 (Holotype:

ANSP 253088; Type Locality: Zanzibar, designated by Abbott 1967).

Strombus (Canarium) ochroglottis betuleti Kronenberg, 1991, p. 54, fig. 1 (Holotype: Kronenberg Collection no. 911; Type Locality: Trincomalee, Sri Lanka, designated by Kronenberg, 1991).

Remarks. *Canarium (Comundrum)* n. subgen. differs from *Canarium sensu stricto* and other genera included in Neostrombini in the short/large angled spire, the compact short body whorl, and the cross section of the lip border. The species *Canarium wilsoni* (Abbott, 1967) have been emended to *C. wilsonorum* by Kronenberg and Dekker (2000), following article ICZN 32.5.1, on the basis of the fact that Abbott dedicated the species to two different unrelated persons. However, the argued change made by Kronenberg and Dekker is unjustifiable and does not increase stability, but rather generated confusion with Petuch's *Strombus wilsonorum*, and should therefore be suppressed. Abbott was aware of the use of -orum for names of couples or family relations (*Conus sennottorum* Rehder and Abbott, 1951, etc.), with the two people referred to by Abbott 1967 not having a relationship guiding his construction of *wilsoni*. We therefore return to the correct published epithet by Abbott (1967), reinstate *Strombus wilsonorum* Petuch, 1994, and suppress *Strombus praeraninus* Kronenberg and Dekker, 2000.

Canarium (Elegantum) Liverani, Dekkers & Maxwell, new subgenus

Type Species. *Strombus erythrinus* Dillwyn, 1817.

Diagnosis. Solid shells with a falcate cross section of the outer lip with a fine ridge forming the outer edge.

Description. The solid shell is elliptic-rhomboid with a teleoconch with variable height

of the spire. The cross section of the labrum is falcate, with a fine ridge forming the outer edge. The columella is well formed the length of the aperture and the liration is variable between species. The inside of the labrum is lirate. The sculpture of the shell: shoulder with axially elongated tubercles and fine spiral cords; last whorl ventral side may have axially elongate tubercles, or axial plicae, dorsal side with axially elongate tubercles.

Etymology. Derived from the Latin *elegans*, meaning elegant, refined, of fine manners, in the neuter singular nominative, in recognition of the elegant shape of the shells within the genus.

Synonymy.

Strombidea Jousseaume, 1888, p. 174 (Type: *Strombus erythrinus* Chemnitz, 1795 = *Strombus erythrinus* Dillwyn, 1817) (preoccupied).

Included Taxa.

Strombus erythrinus Dillwyn, 1817, p. 673 (Lectotype: We designate Chemnitz (1795 p. 195, fig 1874 and 1875); Type Locality: Red Sea (designed by Abbott 1960)).

Strombus elegans Sowerby II, 1842, p. 30, pl. 7, figs. 43 & 48 (Lectotypes: 2 in the NHMUK; Type Locality: The type locality for *Strombus elegans* is not given with the original description, nor does Abbott (1960) give one. Abbott mentions a lectotype ("cotype") from New Caledonia. We therefore designate New Caledonia as type locality. The species is known from South Western Pacific).

Strombus radians Duclos in Chenu, 1844, p. 5, pl. 4, figs. 15 & 16 (Lectotype: Duclos in Chenu, 1844, p. 5, pl. 4, figs. 15 & 16; Type Locality: Japan, designated by Abbott 1960).

Strombus rugosus Sowerby I, 1825, p. 20, no. 1791 (Unknown location of type material (Abbott 1960), but maybe NHMUK (Abbott 1960); The type locality of *Strombus rugosus* is East Indies and is

obviously erroneous. It is a very localised species with records from Fiji, Ellice, Samoa and Tonga (Abbott 1960). We herewith designate as type locality: Tonga, without further refining).

Remarks. *Canarium (Elegantum)* n. subgen. differs from *Canarium* sensu stricto and other genera included in Neostrombini in the strongly sculptured spire, the slender and tuberculated/plicated body whorl, and the cross section of the lip border.

The use of *S. elegans* is often neglected and erroneously replaced by *S. erythrinus* which is an African species. *Canarium radians* is sold in many colour forms from the Philippines, almost always erroneously named *C. erythrinum*, the endemic Red Sea species. *Strombus rugosus* seems to be intermediate between *S. elegans* and the rougher and smaller *S. scalariformis* and *S. hellii* and can be a link in the evolution of these species, from the smoother *S. erythrinus* from the Red Sea to the smaller and coarser species in the eastern range of the genus.

Canarium (Stereostrombus) Liverani, Dekkers & Maxwell, new subgenus

Type Species. *Strombus scalariformis* Duclos, 1833.

Diagnosis. The shell is small and solid, with a labrum cross section that is acuminate and a fine ridge that is extended forming the edge, the columella is coloured and lirate.

Description. Small shells, last two whorls may rapidly increase in diameter giving a fat shape to the shell. The surface of the shell is entirely sculptured spirally by thin cords, and axially by elongated ribs, with stronger tubercles on dorsum of last whorl. The lip is thin formed with a labrum with a cross section that is acuminate and a fine ridge that is extended forming the edge. The inside of the labrum is

lirated, the stromboid notch shallow, adapical part of lip with one or two lobes, of which the one close to the strombid notch is the biggest and often protruding. The columellar callus thick, coloured, margined and lirated.

Etymology. The name is a combination of the Ancient Greek adjective *στερεός* meaning 'solid' as in hard or firm in the masculine singular nominative (as prefix), and the genus *Strombus*.

Synonymy.

Strombus (*Hawaiistrombus*) Bandel 2007, p. 151 (Type: *Strombus helli* Kiener, 1843 = *Strombus hellii* Kiener, 1843) (*nomen nudem*).

Included Taxa.

Strombus hellii Kiener, 1843, p. 59, pl. 13, fig. 2 (Lectotype is NHMUK 1961180; Type Locality: The original type locality of *Strombus hellii* as Mer des Indies, Les cotes de l'île Zanzibar (Kiener 1843, p. 59). This is obviously incorrect as it is endemic to the Hawaiian Island Chain. We herewith designate off Oahu Island, Hawaii as type locality).

Strombus scalariformis Duclos, 1833, pl. 28 (Syntype: MNHN-IM-2000-32462; Type Locality: The original type locality of *Strombus scalariformis* is: *Mers de la Chine*. This was a commonly used origin entry in many descriptions of species in the 19th century and as such of little value. We here designate Reunion island as a more restricted type locality).

Remarks. *Canarium* (*Stereostrombus*) n. subgen. differs from *Canarium* sensu stricto and other genera included in Neostrombini by the sculptured spire and body whorl, the uniformly and strongly coloured columella and the cross section of the lip border.

The morphological results indicate that *Strombus hellii* and *Strombus scalariformis* may share a common ancestor, but information on this subject is lacking.

Maculastrombus Liverani, Dekkers
& Maxwell, new genus

Type Species. *Strombus maculatus* Sowerby II, 1842.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus maculatus* Sowerby II, 1842 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Diagnosis. Shells with a cuneate outer lip and smooth body whorl, the later teleoconch with distinctive tubercles.

Description. The solid shell is elliptic-rhomboid in form and has a teleoconch that is ~ 1/5 the height of shell. The cross section of the labrum is cuneate and there is no labial ridge. The columella is well formed and runs the length of the aperture, with the columella having lirations both posteriorly and anteriorly. The inside of the labrum is lirated. The later teleoconch is tuberculate; a subsutural cord is present. The mid body whorl is smooth with small to obsolete shoulder nodules. The anterior part of the body whorl bears about 12-15 quadrate flattish spiral lines.

Etymology. The name is a combination of the Latin adjective "maculatus" in singular masculine nominative, meaning patterned with spots or blotches, and the genus *Strombus*.

Included Taxa.

Strombus flavidus var. *depauperata*
Dautzenberg & Bouge, 1933, p. 296
(Syntypes: IRNSB IG. 10591; Type
Locality: Makatea, Tuamotus, selected by
Abbott 1960).

Strombus maculatus Sowerby II, 1842, p. 30,
pl. 7, fig. 53 (Syntypes: NHMUK
1969340; Type Locality: Kawaihoa,

Hawaii, originally the Sandwich Islands, but restricted by Abbott 1960).

Canarium rapanuensis Liverani, Wieneke & Kronenberg, 2021, p. 63, pl. 1, figs. 7-10 (Holotype: RMNH. Mol. 178344; Type Locality: La Perousse Bay, Rapa Nui, Chile selected by Liverani *et al.* 2021).

Remarks. *Maculastrombus* n. gen. differs from *Canarium* sensu stricto and other genera included in Neostrombini by the compact spire and body whorl with almost no sculpture, and the cross section of the lip border.

Neostrombus Liverani, Dekkers & Maxwell, new genus

Type Species. *Strombus fusiformis* Sowerby II, 1842.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus fusiformis* Sowerby II, 1842 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Diagnosis. The shell is fusiform with a columella that is diminished posteriorly, with a cuneate cross section of the labrum and lacking a fine ridge at the edge.

Description. Shell solid, relative heavy, fusiform. The type species is from 26 to 45 mm. The height of the teleoconch is ~ 1/4 height of shell. Spire with small former varices. Post nuclear whorls with a sutural cord. The sculpture of the mid body whorl is smooth, but may have obsolete shoulder nodules. The body whorl develops spiral sculpture towards the labrum. Base of the shell with small spiral cords. The labrum in cross section is cuneate without a fine ridge at the edge and has many lirae. Labial ridge present. The columella is lirate, sometimes totally and sometimes the mid-section is smooth. Strombid notch poorly developed. Anterior canal broad and depressed. The inside of the labrum of the shell is lirate.

Etymology. The name is a combination of the Ancient Greek adjective, νέος meaning ‘fresh, youthful or new’ in the masculine singular nominative (as prefix), and the genus *Strombus*.

Synonymy.

Fusicanarium Romagna Manoja 1980, p. 13 (Type: *Strombus fusiformis* Sowerby II, 1842) (*nomen nudem*).

Strombus (*Fusistrombus*) Bandel 2007, p. 151 (Type: *Strombus fusiformis* Sowerby II, 1842) (*nomen nudem*).

Included Taxa.

Strombus fusiformis Sowerby II, 1842, p. 31, pl. 9, figs. 91 & 92 (Holotype: NHMUK n. 1969327; Type Locality: Chumbi Island, Zanzibar, designated by Abbott 1960).

Remarks. *Neostrombus* n. gen. differs from *Canarium* and other members of the Neostrombini in having a columella that is not uniform in form the length of the aperture. The spire of *Neostrombus* n. gen. is high and smooth, the body whorl is slender and smooth, and the cuneate cross section of the lip distinguishes this species.

Neostrombus n. gen is erected to replace two older names, both of which have failed to comply with article 13 of the ICZN (1999), namely *Fusicanarium* Romagna Manoja, 1980 and *Strombus* (*Fusistrombus*) Bandel, 2007.

Terestrombus Kronenberg and Vermeij, 2002

Type Species. *Lambis fragilis* Röding, 1798.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Lambis fragilis* Röding, 1798 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Original Diagnosis. “Small, thin-shelled, spirally and axially almost smooth strombids with rounded, basally unconstricted whorls, thin,

determinate, unglazed outer lip, indistinct stromboid notch, and thin columellar callus” (Kronenberg and Vermeij 2002, p. 49).

Original Description. “Shell small for family (maximum height about 49 mm), fusiform, basally unconstricted on left side opposite outer lip, very weakly constricted at outer lip of adult. Protoconch of about 2.5 smooth whorls. First one to two teleoconch whorls with about eight fine spiral incised lines, other whorls of spire smooth, rounded, little inflated, with or without weak rounded varices. Last whorl smooth except for fine spiral grooves on base. Terminal adult varix present but low, defined by weak axial ridge behind sharp, unglazed edge of lip. Inner (adaxial) surface of outer lip with or without very fine, short spiral striae. Columellar callus thin, narrow, smooth. Stromboid notch on adult outer lip shallow, poorly defined; projection between stromboid notch and anterior canal narrow, pointed. Adapical canal present or absent. Operculum stromboid, elongate, arched, serrated on convex edge” (Kronenberg and Vermeij 2002, p. 50).

Supplementary Description. The teleoconch is approximately 1/5 of the axial height of shell. The shells are thin and fragile. The cross-section of the labrum is falcate and there are no teeth or formed fine ridge on the edge. The columella is weakly formed. The liration of the inner aperture is typically diminished. The shell is smooth and lacking in distinctive sculpture.

Synonymy.

Terestrombus Kronenberg and Vermeij, 2002, p. 49 (Type: *Lambis fragilis* Röding, 1798)

Included Taxa.

Lambis fragilis Röding, 1798, p. 62, no. 792 (Lectotype: Chemnitz 1788, plate 157, fig. 1503; Type Locality: Zamboanga, Mindanao, selected by Abbott 1960).

Strombus terebellatus Sowerby, 1842, p. 31, no. 30, pl. 9, figs. 84 & 85 (Syntypes: NHMUK n. 1969338; Type Locality: Viti

Levu Island, Fiji, selected by Abbott 1960).

Strombus (Canarium) terebellatus afrobellatus Abbott 1960, p. 88, pl. 61 fig. 2 (Holotype: ANSP no 214295; Type Locality: Pange Island, Zanzibar, designated by Abbott 1960).

Remarks. This is a genus of thin walled shells that lacks any major sculpture. The base of the shell is relatively open and this may give the shell a superficial look of some members of the allied Seraphsidae.

Tridentarius Kronenberg and Vermeij, 2002

Type Species. *Strombus dentatus* Linnaeus, 1758.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus dentatus* Linnaeus, 1758 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Original Diagnosis. “Small, high-spined strombids with strongly reduced spiral sculpture, determinate outer lip with glazed adult edge and three sharp basal projections. An indistinct stromboid notch is separating the two abapical most projections. A thick, narrow columellar callus is present, and a long adapical apertural channel” (Kronenberg and Vermeij 2002, p. 51).

Original Description. “Shell small for family (maximum height 56.5 mm), fusiform, basally very weakly or not constricted. Protoconch of about 2.5 smooth whorls. First one to two teleoconch whorls with eight very fine incised spiral lines and fine growth lines. First three to four teleoconch whorls with varices. Later spire whorls with gradually appearing axial ribs, most strongly expressed at periphery, abapically fading out above midpoint of whorl. Determinate adult outer lip little expanded, with glazed edge, adapically extending as narrow apertural channel with the adapical extension of

the thickened, narrow columellar callus. Edge of adult outer lip dentate, the adapical two teeth axially broad and rounded, lobe-like, the abapical three teeth sharp, triangular, spinelike, directed ventrally and abapically. Stromboid notch shallow but distinct, situated between the two abapical-most teeth. Abapical end of inner lip pointed, extending beyond abapical most tooth on outer lip. Columella abapically and adapically with a few indistinct thin plicae. Outer lip very little expanded abaxially, finely spirally striate on inner (adaxial) surface. Aperture narrow, widening abapically. Operculum stromboid, elongate, arched, serrated on convex edge" (Kronenberg and Vermeij 2002, p. 51).

Supplementary Description. The teleoconch is approximately 1/5 of the axial height of shell. The shells are solid. The cross-section of the labrum is falcate and distinctive teeth anteriorly. The columella is well formed the length of the aperture and lirate at both ends. The liration of the inner aperture is well formed. The shell is smooth and lacking in distinctive sculpture.

Synonymy.

Tridentarius Kronenberg and Vermeij, 2002, p. 49 (Type: *Strombus dentatus* Linnaeus, 1758).

Included Taxa.

Strombus dentatus Linnaeus, 1758, p. 745, no. 0 (Lectotype: We designate Chemnitz 1788, pl. 157, no. 1501 and 1502 as the types; We designate Olango Island as the type locality).

Remarks. Linnaeus described the species we now know as *Tridentarius dentatus* in the 10th edition of the *Systema Naturae* on page 745 as no "0" between species 440 (*urceus*) and 441 (*ater* = *Faunus ater* (Linnaeus, 1758), not a Strombidae species). It looks like he added it at a later moment before printing, not altering the numbering he already had used throughout the work. He did not supply a reference for this species which is rather unusual for Linnaeus,

but his description is clear enough. Dodge 1946 who addressed the identity problem of this species was very clear about the unambiguous nature of the species, just as later authors after him. The original description of *Strombus dentatus* reads: *S. testa labro attenuato brevi dentato, ventre spiraque plicatis*. Translated (Dodge 1946): Shell with a "thinned-out" short and toothed lip, body-whorl and spire plicate. Dodge, however, does not mention a type for this Linnean species. Abbott 1960 also refrains of referring to a type. Kronenberg & Vermeij 2002 also remain in silence about a type for this species. According to Dodge 1956 no Linnean type was found, nor was a type locality given.

DISCUSSION

While Abbott 1960 recognised that there are several morphological groups that were distinctly distinguishable within the *Canarium*, his use of the subgeneric rank gave him limited taxonomic ability to formally recognise these. The elevation of *Canarium* to genus has allowed the space within the formal ICZN (1999) for these to be recognised. However, there was much discussion between the authors on whether to define a clade to contain both the *Canarium* (*Stereostrombus*) n. subgen. and the *Canarium* (*Elegantum*) n. subgen.. The decision to not name the clade was based on that there were no officially recognised ranks left. Some authors did not want to inflate the higher taxonomy to fit the nomenclature, even though it was argued, and rejected, that the ICZN (1999) does allow for more informal ranks.

Canarium (*Comundrum*) *klineorum* shares similarities to both the *Canarium* and *Comundrum* subgenera and may be an ancestral form between them. *Canarium klineorum* is a highly geographically restricted, and morphologically stable species, which may indicate a shallow genetic pool of diversity that

has significant impact on the potential for divergence.

CONCLUSION

This revision provides another step in the understanding of the internal relationships within the Stromboidae. The clades identified herein form natural morphological groups that reflect a particular morphological evolutionary pathway unique to each of them, generating a system of nomenclature that reflects the hypothetical relationships, and is at the same time practical in its application, achieved with the use of both a definition and diagnosis. The definition expresses a statement that reflects the understanding of the sister taxa relationships. In contrast, the diagnosis enables the physical recognition of the taxon from other taxa.

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<i>afrobellatus</i>	3	1	1	3	1	1	3	4	1	1	1	1	1	1
<i>anatellum</i>	3	1	2	1	2	1	1	1	3	3	2	1	3	3
<i>betuleti</i>	3	1	2	1	3	1	1	2	3	3	1	1	2	2
<i>daveyi</i>	3	2	2	1	2	1	1	1	3	3	2	1	3	3
<i>dentatus</i>	3	1	2	3	1	2	1	1	3	3	2	1	2	2
<i>depauperatus</i>	3	1	2	3	1	1	1	1	3	1	1	1	2	2
<i>elegans</i>	3	3	2	3	4	1	1	2	4	3	2	2	3	3
<i>erythrinum</i>	3	2	2	3	4	1	1	2	4	3	2	2	3	3
<i>esculentum</i>	3	2	2	1	2	1	1	3	3	3	2	1	1	1
<i>fragilis</i>	3	1	1	3	1	1	3	1	1	3	1	1	1	1
<i>fusiformis</i>	1	2	2	2	1	1	2	1	4	2	1	1	1	1
<i>geelvinkbaaiense</i>	3	2	2	3	2	1	1	1	3	3	2	1	3	3
<i>hellii</i>	2	2	2	4	4	1	1	1	2	2	2	2	3	3
<i>incisum</i>	3	1	2	1	2	1	1	1	3	3	1	1	3	3
<i>klineorum</i>	3	2	2	1	3	1	1	2	3	3	3	1	3	3
<i>labiatum</i>	3	2	2	1	2	1	1	1	2	3	2	3	3	3
<i>maculatus</i>	3	1	2	3	1	1	1	1	3	1	1	1	2	2
<i>manintveldi</i>	3	1	2	1	2	1	1	1	3	3	2	1	3	3
<i>microurceus</i>	3	1	2	1	3	1	1	2	2	2	1	1	2	2
<i>mutabile</i>	3	1	2	1	3	1	1	1	2	2	1	1	2	2
<i>ochroglottis</i>	3	2	2	1	3	1	1	2	3	3	2	1	2	2
<i>olydium</i>	3	2	2	1	2	1	1	1	2	3	2	3	3	3
<i>orrae</i>	3	2	2	1	2	1	1	1	3	3	2	3	3	3
<i>ostergaardi</i>	3	1	2	1	3	1	1	2	3	2	1	1	2	1
<i>radians</i>	3	2	3	3	4	1	2	3	2	3	2	2	3	3
<i>rapanuensis</i>	3	1	2	3	1	1	1	1	3	1	1	1	2	2
<i>rugosum</i>	3	2	2	3	4	1	1	1	4	1	2	2	3	3
<i>scalariformis</i>	3	2	2	4	4	1	1	1	2	2	2	2	3	3
<i>terebellatus</i>	3	1	1	3	1	1	3	4	1	2	1	1	1	1
<i>urceus</i>	3	2	2	1	2	1	1	3	3	3	3	1	3	3
<i>wilsoni</i>	3	1	2	1	3	1	1	1	3	3	2	1	2	2
<i>youngorum</i>	3	2	2	3	2	1	1	1	3	3	2	1	3	3

Table 1. Characteristics and coding used to determine species relationships. Form of shell (A): fusiform (1); orbicular (2); elliptic-rhomboid (3). Teleoconch height (ventral) (B): ~ 1/5 height of shell (1); ~ 1/4 height of shell (2); ~ 1/3 height of shell (3). Shell thickness (C): fragile (1); solid (2). Cross section of the labrum (D): spatulate (1); cunicate (2); falcate (3); acuminate (4). Cross section of labrum with fine rim ridge (E): absent (1); located centrally (2); located on the inner edge (3); forming outer edge of labrum (4). Labrum with teeth (F): absent (1); present (2). Columellar callus (G): well-formed the length of aperture (1); diminished posteriorly (2); diminished (3). Columella colouration (H): single colour (1); axially bicoloured (2); variability flushed with colour (3); diminished columella (4). Columella liration (I): absent (1); completely lirate (2); anteriorly and posteriorly lirate only (3); specimen dependant (4). Aperture colouration (J): white (1); colouration only where lirate (2); coloured (3). Ventral body whorl shoulder sculpture (K): smooth (1); nodules which may form shoulder plications, these may be diminished (2); strongly knobbed (3). Central ventral body whorl (L): smooth (1); axially ribbed (2); variable (3). Mid-teleoconch sculpture (M): smooth (1); tuberculated, which may be axially compressed and elongated (2); axially plicated (3). Sculpture of penultimate whorl (N): smooth (1); tuberculated, which may be axially compressed and elongated (2); axially plicated (3).

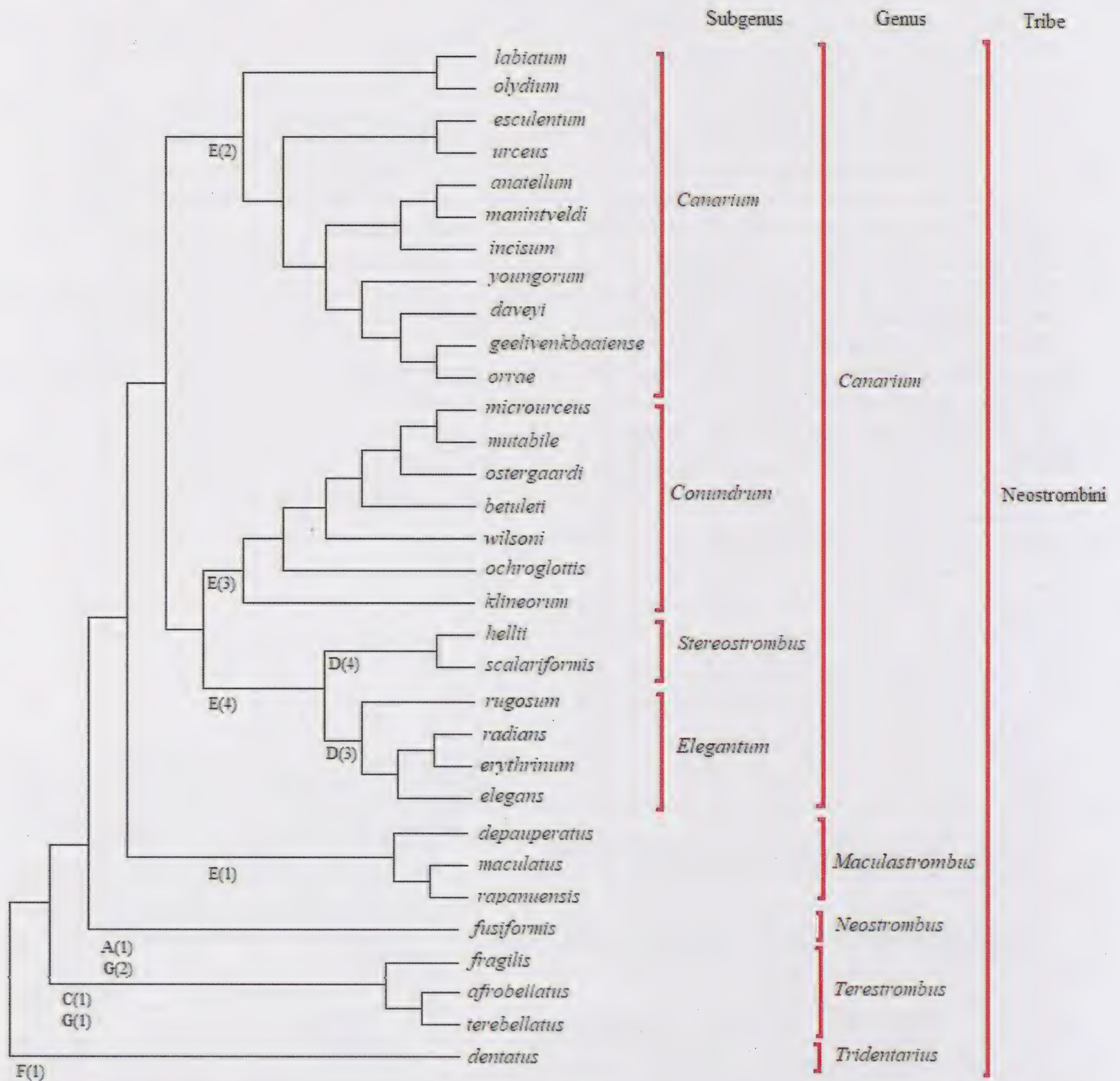


Figure 1. Neostrombini n. tribe showing the clusters of species and proposed names for those clusterings, with important defining character states inserted.



Figure 2. Apertures of members of *Canarium* (genus) grouped by sub-clade membership.



Figure 3. Apertures of members of *Neostrombini* grouped by clade membership excluding *Canarium*.

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Are the ICZN and PhyloCode that incompatible? A summary of the shifts in Stromboidean taxonomy and the definition of two new subfamilies in Stromboidae (Mollusca, Neostromboidae)

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ABSTRACT The taxonomy of Stromboideans has, historically, been simplistic. However, recent revisions have seen new taxa introduced to distinguish relationships between species clusters. We discuss these numerous advancements in Stromboidean systematics, and describe two new subfamilies here. The key diagnostic characteristic, the basal peg on the first lateral tooth, splits the Strombidae into two clades similar to those observed with molecular data. In defining the new subfamilies, Neoaligerinae and Neostrombinae, we demonstrate that the practical application of the International Code of Phylogenetic Nomenclature (PhyloCode 2020), can also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). This revision further advances and strengthens the framework of Stromboidean nomenclature such that it is able to reflect the current understanding of the evolutionary relationships between members of the Stromboidea.

KEY WORDS ICZN, Neoaligerinae, Neostrombinae, PhyloCode, Sub-family, Stromboidea, Taxonomy, Crown Clade

INTRODUCTION

Historically the taxonomy of Stromboideans has been simplistic based on the utilisation of the taxonomic ranks of family, genera, and subgenera only (Figure 1). However, recent revisions of Stromboideans in Maxwell *et al.* (2020), Dekkers and Maxwell (2020) and Liverani *et al.* (2021) saw taxa introduced to distinguish the finer relationships between species clusters. These revisions were based on the principles of phylogenetic taxonomy, or the use of a relational definition in association with the normal diagnosis. Therefore, there revisions were compliant with both the guidelines of the International Code of Zoological Nomenclature (ICZN 1999) and the principles of the International Code of Phylogenetic

Nomenclature (PhyloCode 2020). The purpose of erecting these taxa was to “demonstrate that nomenclature can reflect the current evolutionary understanding within that complex rather than the simple aggregation of taxa based on uncritical analysis of form alone” (Dekkers and Maxwell 2020, p. 40). The authors therein demonstrated the hypothetical evolutionary relationships used to underpin the proposed nomenclature can be formed under the framework of the ICZN. While there has been some resistance to the acceptance of the PhyloCode, the use of its diagnosis and description for the discernment of higher taxonomic meaning in the structure of the nomenclature does remain compliant with ICZN requirements (Maxwell *et al.* 2019, 2020; Dekker and Maxwell 2020; Liverani *et al.* 2021).

The application of the PhyloCode by Maxwell *et al.* (2019, 2020), Maxwell and Dekkers (2020) and Liverani *et al.* (2021), with the inclusion of a definition for taxonomic rank, shows a path to overcome the formulative rigidity of the ICZN's methodological approach to the construction of the nomenclature, without affecting its application in practice. The definition brings a statement of relatedness when formulating a new taxon and seeks to explain its relationship between closely related taxonomic outgroups. These two codes of nomenclature are not mutually exclusive, and the PhyloCode can be used for the formulation and defining process of identifying and defining clades that are then constructed to conform to the ICZN (Maxwell *et al.* 2019, 2020). It is this definition that allows clades to be reliably knitted into a hypothetical phylogeny. This placement allows us to draw a relational framework between those defined taxa. Similarly, when dealing with those taxa that have not been defined, they should not be included in the phylogeny or the taxonomy, other than given the rank applied per the pre-revision state, and they should be treated as undefined.

Crown clades are defined by using living taxa and their current hypothesised relationships. However, this does not mean that ancestral relatives are excluded. They are recognisable in the structure of the clade name, typically with the prefix 'Neo+' (Maxwell *et al.* 2019). The role of a crown clade is to form a tree-like structure based on extant evidence upon which the fossil branches can be attached. The use of extant taxa to define higher taxonomy provides the taxonomist with evidence, such as anatomy and genetics, for ancestral relationships, which gives a level of robustness to those relationships that are used to generate the phylogeny. The fossils can then be added where they appear to support the evolution of organisms that gave rise to what we see today, as with the case of

Aligerini Maxwell, Dekkers, Rymer and Congdon, 2020. It is therefore wrong to assume that a crown clade does not include fossil taxa because they are omitted from the definition. Importantly, the definitions used to highlight relationships between taxa are not rigid, and are able to be modified as further information and understanding of those relationships becomes apparent. The rejection of crown clades based on the use of structural definitions and the belief that those definitions exclude fossil taxa, not only shows a lack of understanding of what crown clades are but seeks to collapse the taxonomy such that it reverts to some twentieth century simplified state and is, theoretically, retrogressive.

There are two areas of Stromboidean taxonomic practice that have generated considerable public debate: 1) the revisions to the nomenclature that have been undertaken, and are necessary to enable Stromboidean taxonomy to move forward; and 2) the use of the International Code of Phylogenetic Nomenclature (PhyloCode 2020), and how its practical application can also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). In conjunction with the demonstrated reconciliation of the PhyloCode and ICZN practice, we present the current hypothetical state of Stromboidean taxonomy showing practically how these two systems are compatible. Furthermore, we outline the benefits of crown clades for the definition of higher taxa, and particularly that extant taxa are not excluded from inclusion in clades defined with the use of the PhyloCode by the sole use of extant taxa to formulate those definitions. This will be achieved through the recognition of two crown clades within Strombidae.

METHODS

The two clades represent two divergent evolutionary lines in radula development. One line has developed a basal peg on the first lateral tooth, and a second evolutionary line has no basal peg. The taxa without a basal peg tend to be larger than those with basal pegs. The clade of taxa with the basal peg can be distinguished from those without a peg genetically in most cases (Latiolais *et al.* 2006; Irwin *et al.* 2021); only *Conomurex* Fischer, 1884, a taxon with a basal peg, did not conform, and its placement is discussed below.

Clade recognition and name construction followed principles of Bryant (1996) outlined in Maxwell *et al.* (2020). The names circumscribed herein follow the practice of Maxwell *et al.* (2019) with the use of the prefix “Neo+” designating that a crown clade is being described. The ICZN (1999) makes no comment on the use of prefixes.

The taxonomy presented is an amalgamation of the definitions and their relationships for each clade (Maxwell *et al.* 2019, 2020; Dekkers and Maxwell 2020; Liverani *et al.* 2021; Irwin *et al.* 2021). Where taxa have not been defined they have been aggregated at the same status as their sister taxa; not all undefined taxa have been listed in the figures.

SYSTEMATICS

Phylum: Mollusca Linné, 1758

Order: Sorbeoconcha Ponder & Lindberg, 1997

Superfamily: Stromboidea Rafinesque, 1815

Neostromboidae Maxwell, Dekkers, Rymer
& Congdon, 2019

Type Genus. *Strombus* Linné, 1758.

Original Definition. “The clade is nested within Stromboidea, with the characteristics outlined in the diagnosis, and contains taxa more closely related to *Strombus pugilis* Linné, 1758 (Strombidae), *Terebellum terebellum* (Linné, 1758) (Seraphsidae) and *Tibia fusus* (Linné, 1758) (Rostellariidae) than Struthiolaridae Gabb, 1868 and Aporrhaidae Gray, 1850” (Maxwell *et al.* 2019) (Figure 2).

Diagnosis. Eyes positioned distally on peduncles that also have the cephalic tentacle attached.

Original Description. “The animal possesses eyes on the end of the peduncles. The cephalic tentacle is also located on the peduncle towards the distal end. The radula has a central rachidian tooth with three lateral teeth either side. The foot is laterally compressed, with a defined propodium and a metapodium. The shell form changes upon maturation with the development of an outer lip structure” (Maxwell *et al.* 2019).

Remarks. The epifamily Neostromboidae incorporates an evolutionary line where the eyes of the animal have evolved to be on the end of peduncles. There are three extant clades incorporated within the Neostromboidae.

Strombidae Rafinesque, 1815

Type Genus. *Strombus* Linné, 1758.

Definition. The clade is nested within Neostromboidae, with the characteristics outlined in the diagnosis, and contains taxa more closely related to *Aliger gigas* (Linné, 1758) (Neoaligerinae n. subfam.) and *Strombus urceus* (Linné, 1758) (Neostrombinae n. subfam.) than to *Terebellum terebellum* (Linné, 1758) (Seraphsidae) and *Tibia fusus* (Linné, 1758) (Rostellariidae).

Diagnosis. Shell with a body whorl that is longer than the combined teleoconch, stromboidal notch well formed, and body whorl sculpture may vary significantly from that of the teleoconch.

Original Description. “2. S. F. *Strombia*. Les Strombiens. Bord de la base ou bouche, dilaté en aile latérale. G. 15. *Strombus* L. 14. *Pterocera* Lam. 17. *Rostellaria* Lam.” (Rafinesque, 1815, p. 145).

Remarks. This family historically contained a number of genera that have now been elevated to family level: *Terebellum* (Seraphsidae) and *Tibia* (Rostellariidae). Similarly, the subgenera have all been elevated to genera.

Neostrombinae Maxwell & Rymer,
new subfamily

Type Genus. *Canarium* Schumacher, 1817.

Definition. Contains all recent and ancestors of Dolominini Dekkers and Maxwell, 2020 and Neostrombini Liverani, Dekkers and Maxwell, 2021 and does not include those ancestors more closely related to members of Neoaligerinae n. subfam. (Figure 3)

Diagnosis. There is a basal peg on the radula first lateral tooth.

Description. The shells are small to medium in size. The posterior canal is straight and extended. There is basal peg on the first lateral tooth. Dorsum of the body whorl often smooth or with limited shoulder ornamentation.

Etymology. The name is formed from the combination of the genus *Neostrombus*, as “Neo+strombus+” where the prefix “Neo+” is also used to denote a crown clade, and the subfamily suffix “+inae” is used to reflect the taxon’s position within the nomenclature.

Remarks. This clade is able to be recognised in the published gene trees (Latiolais *et al.* 2006). One taxon however, did not conform to this character based hypothesis. *Conomurex* fell genetically within the taxonomic cluster of Neoaligerinae n. subfamily. However, the presence of the basal peg on the first lateral tooth requires it to be contained with Neostrombinae n. subfam. where it forms the basal taxon within this hypothesised taxonomy,

although this placement is contested with mitochondrial analyses (Latiolais *et al.* 2006; Irwin *et al.* 2021). While there is no anatomical evidence available on the radula formula, the general similarity for *Barneystrombus* Blackwood, 2009 in the formation of the outer lip conforms to the morphology of other members of the Neostrombinae. However, exact relationships are unclear, and *Barneystrombus* is treated as currently undefined (Figure 3). The positions of *Conomurex* and *Laevistrombus* Abbott, 1960 are undefined, but these taxa possess a basal peg on the radula’s first lateral tooth.

Neoaligerinae Maxwell & Rymer,
new subfamily

Type Genus. *Aliger* Thiele, 1929.

Definition. Contains all recent taxa of the most common ancestors of Aligerini Maxwell, Dekkers, Rymer and Congdon, 2020 and Persististrombini Maxwell, Dekkers, Rymer and Congdon, 2020 and does not include those ancestors more closely related to members of Neostrombinae n. subfam. (Figure 4).

Diagnosis. There are no basal pegs on the radula first lateral teeth. Body whorl dorsum often well ornamented with axial chords, knobs or plaits, flaring or ornamented outerlips.

Description. The shells are medium to large in size. The posterior canal may be extended.

Etymology: The name is formed from *Aliger* Thiele, 1929, as “+aliger+”, and the prefix “Neo+” here used to denote a crown clade, and the subfamily suffix “+inae” to reflect the taxon’s position in the nomenclature.

Remarks. This clade has no basal peg on the first lateral tooth, and are generally of a larger size than members of Neostrombinae. As this clade undergoes revisions, further natural clusters will be found and it is expected that the definitions will need to be amended (Figure 4).

DISCUSSION

The two new clades erected in this paper, combined with those taxa that have previously been defined, provide a sound structural framework upon which the undefined stromboidean taxa can be integrated as reviews are completed. However, while there are murmurings in the Mordorian Halls for a return to a more simplified state of higher taxonomy, to do so would lose the evolutionary meaning that has been achieved with recent revisions, with the loss of definitions contained therein. Therefore, the benefits for understanding the relationships between the different branches of stromboideans cannot be so flippantly disregarded based on a “clutter” argument, unless this heralds a call to return to the dark ages of mass synonymisation of much of stromboidean taxonomy. The integrated use of the PhyloCode and ICZN has been demonstrated to illustrate significant advancements in the understanding of stromboidean systematics.

The difference in the application of the codes with the formulation of names is the use of the first part of the binominal. The ICZN requires the use of the genus for this position, while the PhyloCode (Article 21) “is independent of categorical ranks (Art. 3.1), the first part of a species binomen is not interpreted as a genus name but simply as the name of a taxon that includes that species”. In practice, under the ICZN the need to state the specific rank of genus to form a binominal means that a sample taxon *Canarium (Stereostrombus) hellii* Kiener, 1843 would have to have its ranks below genus listed in brackets. In contrast, the applied PhyloCode may have the same taxon as *Stereostrombus hellii* Kiener, 1843, which ties the first part of the binominal name to the lowest cladistic rank. Another notable difference between the codes when applied is

the convention for all equivalent intermediary ranks to be recognised implicitly under the ICZN and the understanding that these are irrelevant, being a repetition of the higher rank, and practically omitted when working within the PhyloCode.

CONCLUSION

We argue that the PhyloCode and ICZN are not mutually exclusive, and that the use of ICZN conforming taxonomy, with the inclusion of a definition, does not exclude either taxonomic systems, but rather improves the ability to bring evolutionary meaning to the nomenclature. We have demonstrated that the use of crown clades forms a strong framework upon which the taxonomy of complex systems can be constructed, and that they do not exclude fossil taxa by their definitional structure. As more revisions of this superfamily are undertaken, there will be a need to utilise other ranks, such as supertribe. The lack of use of these ranks in molluscan studies should not preclude their introduction, as to do so would limit the taxonomist’s ability to bring evolutionary and relational meaning to the nomenclature.

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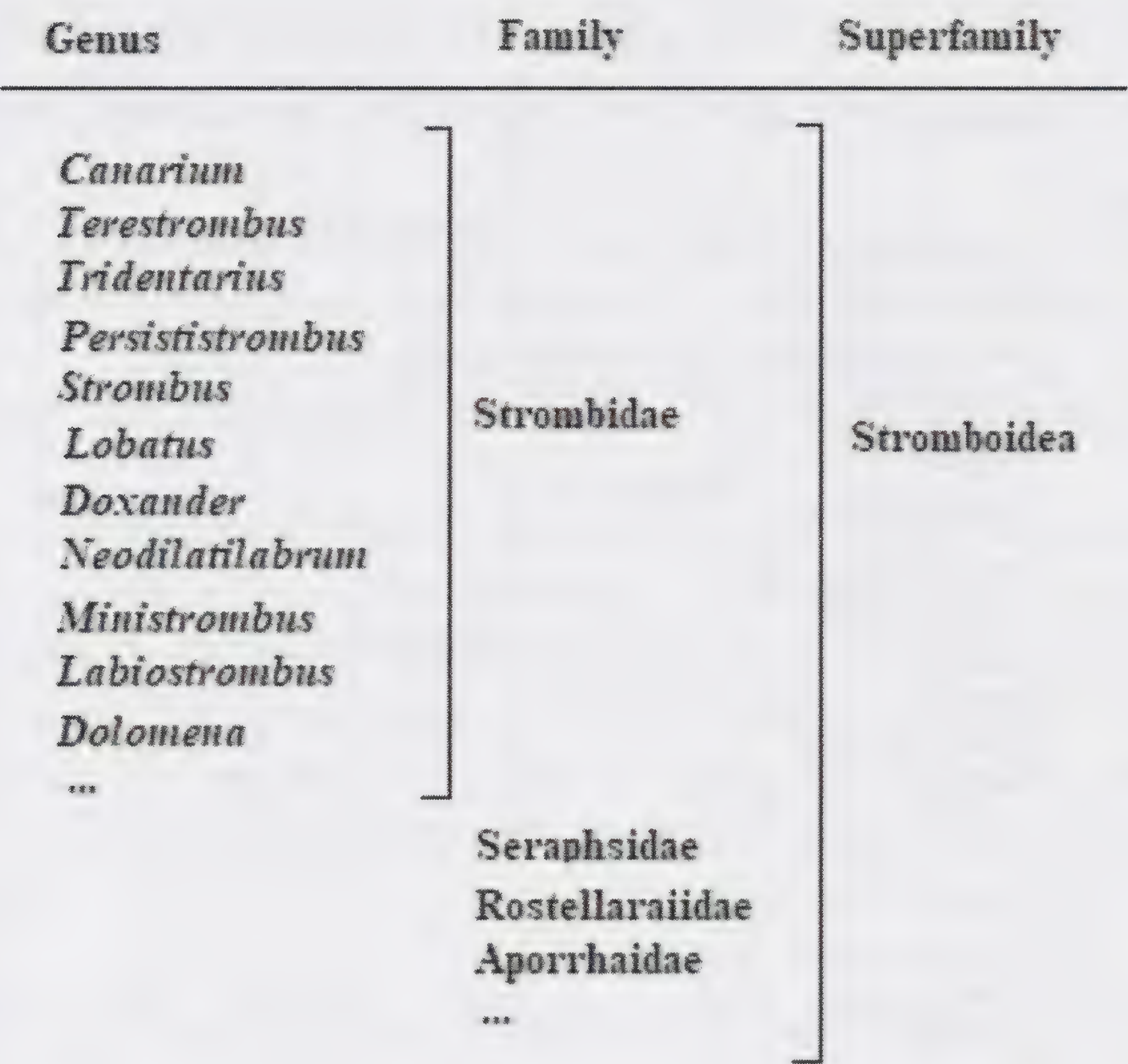


Figure 1. The historical arrangements of Stromboidea (Abbott 1960; Liverani 2013).

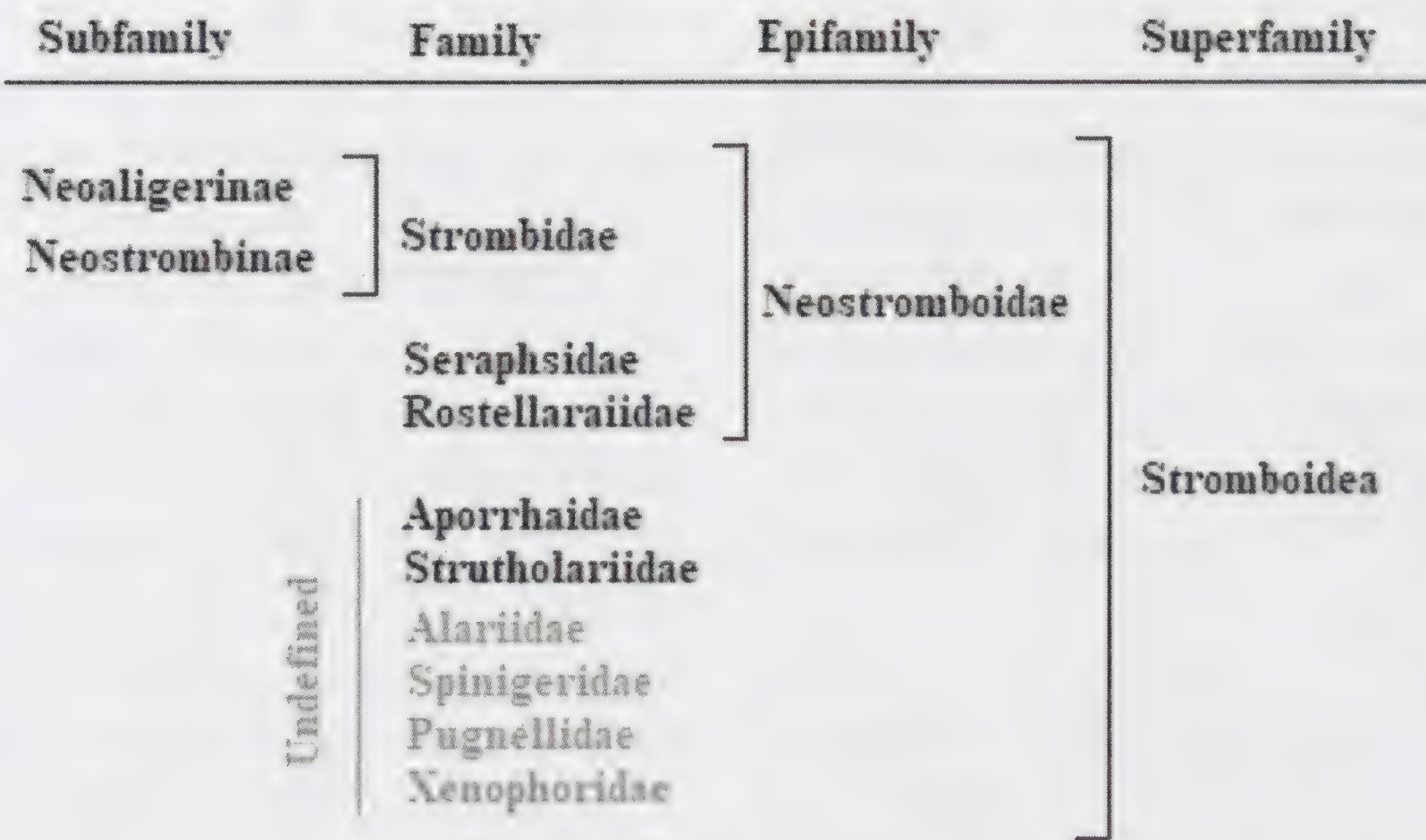


Figure 2. The hypothesised phylogeny of Neostromboidea (Maxwell *et al.* 2019; Irwin *et al.* 2021).

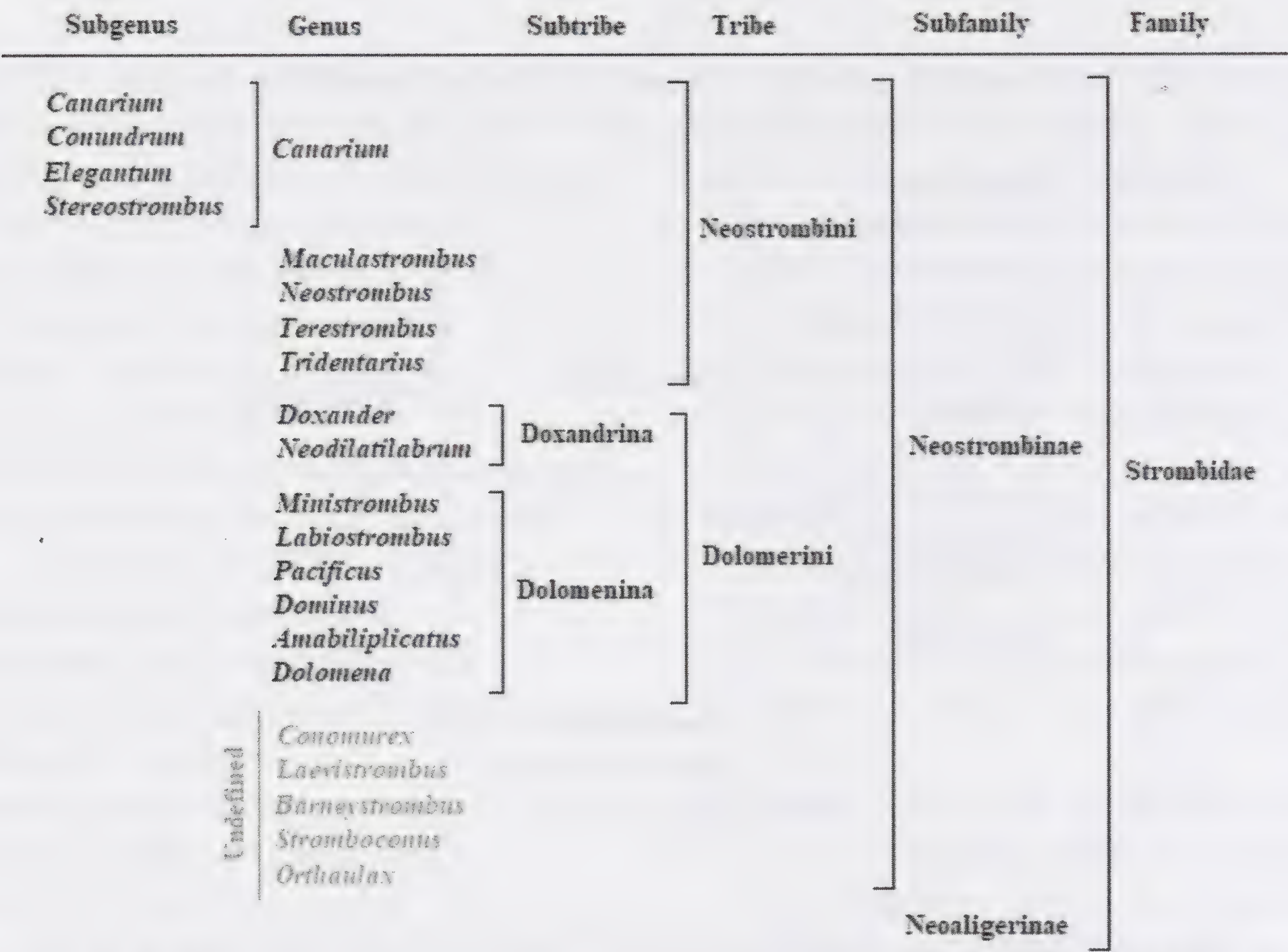


Figure 3. The hypothesised phylogeny of Neostrombinae n. subfam. (Dekkers and Maxwell 2020; Liverani *et al.* 2021).

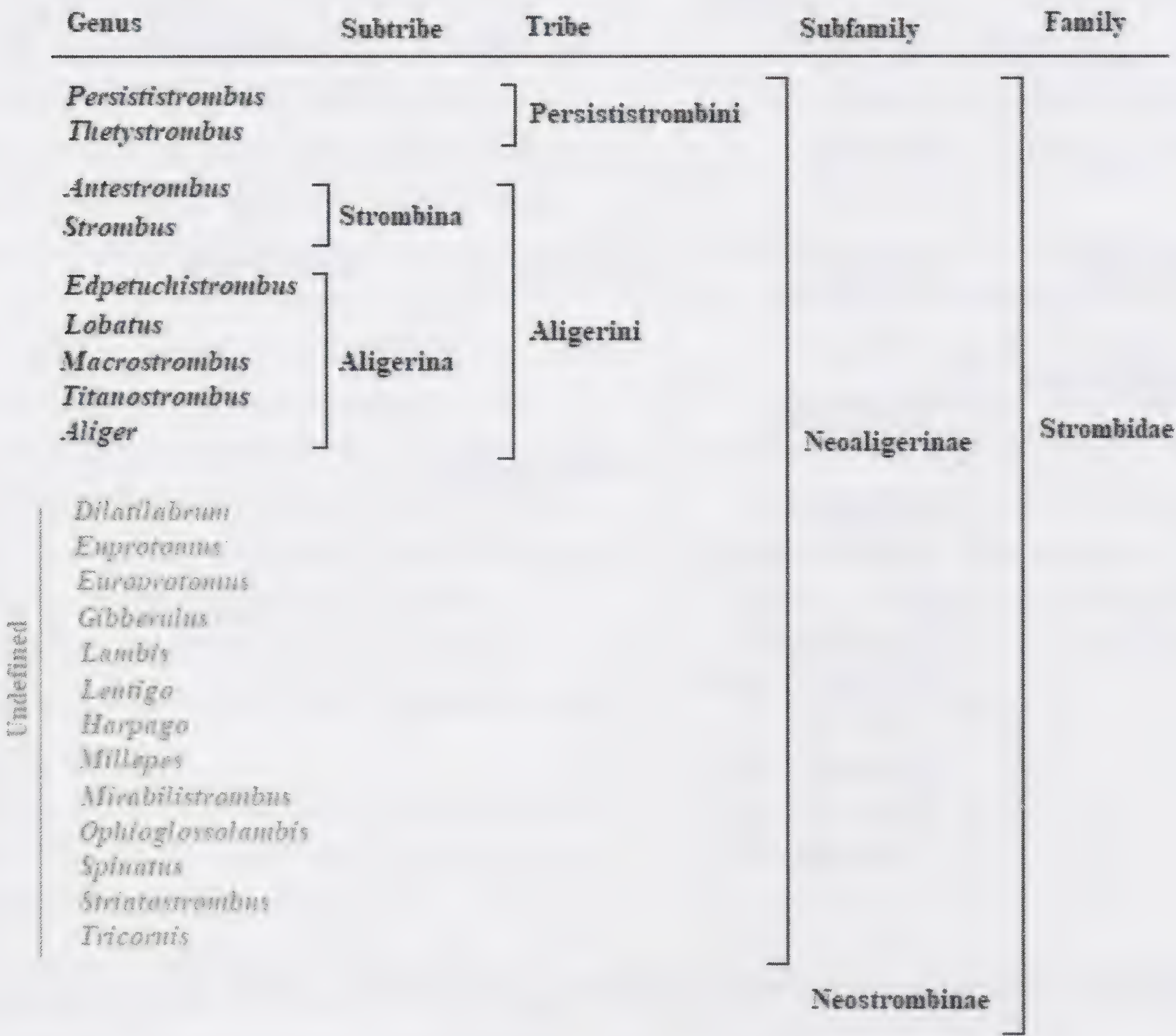


Figure 4. The hypothesised phylogeny of Neoaligerinae n. subfam. (Maxwell *et al.* 2020).

New Records of *Polymita venusta* (Gmelin, 1792) Populations in Northern Foothills of Sierra de Boniato, Santiago de Cuba Province

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ABSTRACT Three new localities of *Polymita venusta* are uncovered from the northern foothills of Sierra de Boniato in the Santiago de Cuba province. In those, five new populations inhabiting fragmented forests over karstic substratum were found between 238-405 meters above sea level. The rediscovery of a unique color form took place in one colony from the La Luz vicinity. These populations occupy a highly deforested area where the main activities are cattle grazing and agriculture, combined with other anthropic threats. Protected Areas planning for this human highly disturbed zone is nonexistent.

KEYWORDS Cuban land snails, Cepolidae, *Polymita*, *Polymita venusta*, tree snails, Sierra Maestra, Seirra de Boniato

INTRODUCTION

Polymita venusta (Gmelin, 1786) (Cepolidae), is an endemic and endangered Cuban land snail recognized by its beautiful shell and high chromatic polymorphism. It is the most widespread of all the species in the genus, and seemingly survives in no more than 20 karstic vicinities throughout Santiago de Cuba province. The main confirmed habitat regions in this province are the karstic areas of La Mella's Quarry (Mella municipality, south foothills of Altiplanicie de Nipe), Baire-La Tabla-Los Negros-Maffo (NW Tercer Frente municipality, northern foothills of Sierra del Turquino) and the coastal marine terraces southeast of Santiago de Cuba municipality (Meseta Cársica de Santiago de Cuba) (Maceira, 2000; Maceira *et al.*, 2009), this latter region is covered largely by xerophytic shrub and microphyll semideciduous forest. However, there are no records of this species in the scientific literature from other mountain regions such as Sierra de La Gran Piedra, Sierra de Boniato, and Cauto

river plains basin, with exception of the isolated population found in Monte Barranca forest (Palma Soriano municipality) (reported by Cardona *et al.*, 2009 and Méndez-Hernández, 2009).

Few of those areas contain large populations with high densities. Yet, the majority of the recorded populations of *P. venusta* in that eastern province of Cuba are small low density colonies scattered in patches. However, records from old collections echo how dense those populations once were. Even though, it is difficult to grasp the magnitude of habitat loss and forest fragmentation that these tree snails witnessed since the 18th century, today this species is in the Santiago de Cuba province extent. As commonly happens, recorded localities of any land snails are associated with the interest in publishing those findings by the collectors. If they are not published, and location information can only be found on Museum labels or in research theses that are never published, it becomes difficult to confirm

the extant and endangered populations, decreasing all possible conservation efforts.

Described formerly by J. F. Gmelin in 1792 (but illustrated before in 1786) this species type locality was in fact reported by C. de la Torre in his 1950 posthumous monograph of the genus (Torre, 1950, p.14). Torre, had named this species, in his earlier manuscript accounts, *Helix picta rubrolimbata* and *Helix picta rubrocincta*, and placed *P. venusta* at “Provincia de Oriente, menos los términos de Baracoa y Sagua de Tánamo” (Eastern province, except the Baracoa and Sagua de Tanamo vicinities). Hence, the first locality mentioned of *P. venusta* by Torre from Santiago de Cuba was Aguadores, the place where he considered the *typical form* to inhabit. Other localities from this province were mentioned and can be found on specimen labels from between 1912 and 1952 (e.g. Carretera Central, Finca de Borrero, cerca de Charco Mono, Finca Santa María, El Cobre, Finca La Rosita de los hermanos Borrero, Barrio de Río Frío, Lagunas cerca de Aguadores, Jarahueca, Central Miranda, Cayo del Rey, Siboney, etc.). Years after, from 1987 to 2017, more localities and populations of *P. venusta* from this province were recorded and reported (e.g. Sardinero, Monte Barranca, La Tabla, etc.).

In this paper we discuss only the new records and color varieties of *P. venusta* from San Luis municipality, specifically those located in Sierra the Boniato, an area belonging to Sierra Maestra mountain range, located north of the Tectonic Basin of Santiago de Cuba (Núñez & Viña, 1976). The only new recorded population we could not reach to study was north of Magueyal de San Luis.

MATERIALS AND METHODS

The five *P. venusta* populations were found during field trips conducted from June to September of 2018, in three new localities, all from the Sierra de Boniato north side, southern boundaries of the Cauto high plains, San Luis municipality, Santiago de Cuba province (see Figure 1).

All the collected specimens were placed in the malacology collection of the Zoology Department at Centro Oriental de Ecosistemas y Biodiversidad (BIOECO) in Santiago de Cuba city. Other specimens collected in a subsequent field trip (i.e., July, 2019) were bestowed to the Universidad de Oriente Malacology group for lab research. This group belongs to the Biology-Geography Department, also located in Santiago de Cuba city.

We use Reyes (2011-2012) criteria to designate vegetation types, and the host plants names were updated from Greuter & Rankin (2016).

DISCUSSION

New documented populations description

El Tablón-La Estrella [N20°07'35,2099"/W75°51'28,0199"] [405 meters above sea level (masl)]. This population is 2 km south of the town of El Tablón, on the road to the town of La Estrella, in an area probably less than 0.01 km² of extent. As in the other two locations, the specimens were found in a semideciduous mesophyll forest ecotope, specifically in the secondary vegetation; predominantly *Vachellia macrachanta* (Humb. & Bonpl. ex Willd.) Seigler & Ebinger (Fabaceae). The main host-plants were *Erithalis fruticosa* L. (Rubiaceae), *Chrysophyllum cainito* L. (Sapotaceae), *Thouinia trifoliata* Poit. (Sapotaceae), and *Comocladia platyphylla* A. Rich. ex Griseb

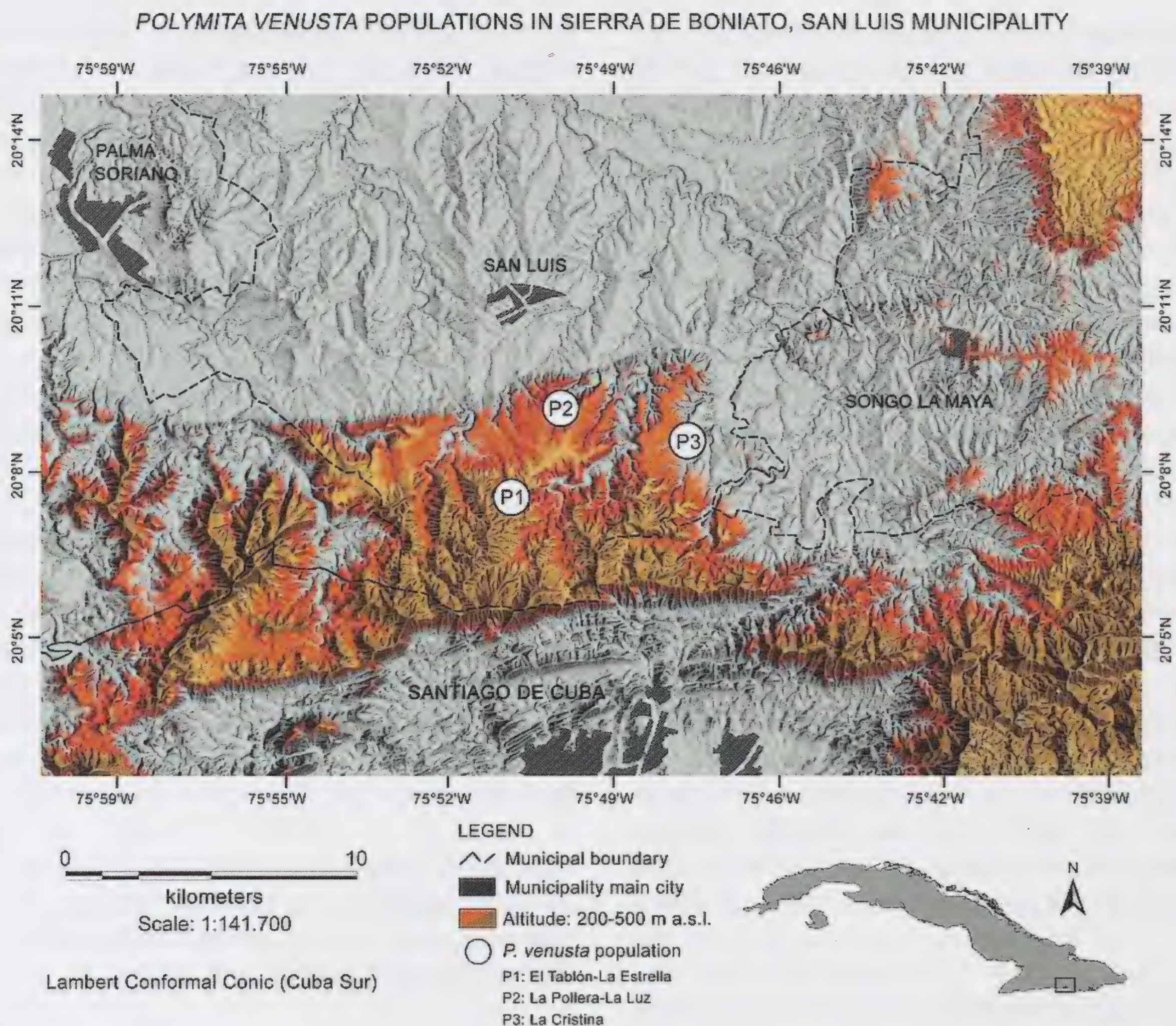


Figure 1. New records of *Polymita venusta* populations in Sierra de Boniato, San Luis municipality.

(Anacardiaceae). Color variations found in this locality include: light yellow with whitish-yellowish sutural and lip band, sometimes with faint banding and specks; typical with specimens sometimes having the bright red sub-sutural and lip band observed in the premature *P. venusta sanguinolenta* (bloody) color form (Torre mss.) (see Figure 2).

La Pollera in La Luz [N20°09'12,2529"/W75°50'33,1125"] [312 masl]. This locality is near the town of La Luz and 2.3 km northeast of El Tablón. This is a small population found in

0.04 km² of extent, 3.1 km N-NE of the El Tablón-La Estrella population and 3.4 km N-NW of the La Cristina population. The area is an abandoned chicken farm (*pollera*) mostly covered by *V. macrachanta*, *Dichrostachys cinerea* (L.) Wight & Arn. (Mimosaceae), *Bursera simaruba* (L.) Sarg. (Burseraceae) and some vines (*Smilax* sp.), which are apparently the main resting substratum for *P. venusta* in this locality. *P. venusta* shares habitat in this locality with other tree snails of the same family, *Coryda alauda* (Férussac, 1821) and *Hemitrochus cesticulus* (Gundlach in Pfeiffer,

1858). Color variations found in this locality are similar to the two morphs found in the El Tablón-La Estrella locality. A third morph, similar to the other two but with a dark sub-sutural band, appeared in this location, rarely with a dorsal thin brownish line. This color variety was indistinctively baptized in manuscript letters by Torre as *nigrosuturalis* or *fuscusuturalis* (from C. de la Torre letters to C. T. Ramsden 1911-1915, deposited at Museum of Natural History C. T. Ramsden at Santiago de Cuba University; also J. F. Milera in 1987 mentions this name but not as *nova ssp.*) (see Figure 3).

Remarks: *P. venusta* color form *nigrosuturalis* or *fuscusuturalis* only occurred in Santiago de Cuba province in a small span from Sierra del Cobre to Sierra de Boniato. In the early-mid 20th century, the area of Sierra del Cobre was subject to *Polymita* over-collecting and today there is no record of any surviving colonies (at least in the last 40 years or so, R. Teruel, personal communication). This likely means that the last population containing this color form is in La Luz!

La Cristina [N20°08'28,7160"/W75°48'44,2378"] [238 masl]. This population is located in a 1.5 km² radius, near to the town of La Cristina about 5 km northeast of the El Tablón-La Estrella population. Three apparently isolated populations were identified, all of them dispersed due the high anthropogenic fragmentation, which includes an active chicken farm to the south, and a slab mining area approximately 1 km to the east (Trinidad's quarry). Specimens were found on shrubs and vines, such as *Ipomoea violacea* L. (Convolvulaceae), but in some places there was a noticeable preference for the non-native *Euphorbia lactea* Haw. (Euphorbiaceae). This preference seems to be recurrent in this species (Santos-Chacón, 2000). Color variations found

in this locality include: light yellow with whitish-yellowish sutural and lip band, sometimes with faint banding and specks; typical bright yellow with sub-sutural and lip bright red band (see Figure 4).

All the reported populations were found in human disturbed areas. Considerable forest loss and nearby human built barriers, such as massive construction sites and wide roads used by trucks for wood extraction or public transport, contributes to lethal dust contamination of *P. venusta* hosts plants (see Figure 5).

Depending on age, habitat features and forest fragmentation, *P. venusta* specimens can range in length from 11-12 mm to 26-28 mm, but average length can be considered to be between 17-22 mm (González-Guillén, A. 2014; González-Guillén, A., in prep.). In the newly recorded localities, the sizes are small, 20 mm, more or less.

Populations with a high diversity of color forms are not frequent in Santiago de Cuba province. The exceptions today are Monte Barranca and Cantera de Mella (Mella's Quarry).

The predominant color in all the newly recorded populations is light to bright yellow. Other new recorded populations in the province seem to follow the same trend. Southern Santiago de Cuba *P. venusta* populations have greenish, gray-bluish, chestnut-red-brownish and yellow banded specimens in low numbers. However, why yellow is the most common key color in *P. venusta* in south-central Santiago de Cuba province is still unknown and cannot be answered by mere abiotic factors (Berovides, *et al.* 1987; Milera, *et al.* 1994). Why the yellow form with a subsutural darker band only exists in a small geographic range between El Cobre and San Luis remains a mystery.

The green and chestnut-red appear together with the yellow color forms most frequently in the northern Santiago de Cuba populations. The other albino, pale colored (*i.e.*, pink, light purplish, light yellow-green, gray-bluish), banded (*i.e.*, *testudinea* and its distinctions) or darker varieties (*i.e.*, very dark *rubiginosa*), are present mostly in the 2 well-known northern populations previously mentioned.

Today, *P. venusta* color forms in the remaining populations display just one or several color variations. This led us to consider that, in the distant past when the species was expanding its domain over eastern Cuba, the morph-chromatism among those earlier populations was likely more diverse than today. The three described varieties of *P. venusta* (*olivacea*, *rubiginosa*, and *testudinea*) and even the manuscript undescribed ones (*testudinaria*, *fasciata*, *albida*, *albina*, *sanguinolenta*, *ferruginosa*, *fuscosuturalis*, *nigrosuturalis*, and *violacea*) (González-Guillén, A., in prep.) do not seem to have unique geographic ranges and often more than one color form can be found on the same plant. Thus, we assume these are merely color forms and not subspecies of *P. venusta*.

Polymita venusta uses a large variety of host plants and is probably the best studied in the last 20 years (Reyes-Tur & González-Rodríguez, 2003; Reyes-Tur, 2004; González-Guillén, A. 2014; Reyes-Tur, *et al.* 2020). The colonies of the three recorded populations mentioned in this paper were connected at one time when the forests covered this area and they likely shared the same plant preferences. But, in La Cristina and La Pollera-La Luz, which are the most damaged from forest loss, these population have learned how to survive using non-native plants. We suspect that the longer and shorter spines of *D. cinerea* and *E. lacteal*, as well as its toxic fluids, have provided some protection for the

tree snails against certain predators. Further, the lichens that appear on the trunks of *D. cinerea* could also be a food source.

Only five Protected Areas in Santiago de Cuba contain *P. venusta* populations in its terrestrial bounds: the Managed Floristic Reserve *Monte de Barranca* (311,4 ha); the Managed Protected Area *Carso de Baire* with 7 613,6 ha; and the Protected Area of Managed Resources *Reserva de la Biosfera Baconao* (66 390 ha in Santiago province), which includes the Ecological Reserve *Siboney-Jutisi* (905,00 ha) and the Protected Natural Landscape *Estrella-Aguadores* (210,30 ha) (CNAP, 2013). However, the bulk of the known surviving populations of this species, are not inside any Protected Area. This is the case with the new populations found in the San Luis municipality. Those colonies are threatened and endangered mainly for anthropic, agriculture, mining, cattle grazing and primary cover forest loss reasons. Its survival in these regions depends on future local government action to preserve this beautiful endemic species. Additional studies are required to clarify those and other ecological aspects, such as behavior and adaptations traits of *P. venusta* in disturbed areas, as a way to promote local conservation efforts and to improve management strategies.

A thoughtful evolutionary response study of *Polymita* tree snails' polymorphism could provide some of the most precise indicators of climate alteration. Its short life-span and disproportionate collecting records since the late 19th century offer an exceptional opportunity to measure color phenotype frequencies, habitat change and thermal reactions. Sadly, such an investigation would require incalculable funds and years to review all the most important museum collections in the United States, Europe and Cuba. But, it is possible to protect all the existing populations, making available its remaining genetic pool for future research.

CONCLUSIONS

In our field trips we found some unrecorded *P. venusta* populations from Sierra de Boniato in the San Luis municipality foothills, which are part of Sierra Maestra mountain range. It was also remarkable to observe how those colonies have endured in places under harsh anthropic pressures, sometimes benefiting from non-native plants.

ADDITIONAL REMARKS

Regrettably, some malacological investigations conducted during the past two decades in eastern Cuba, were embedded with unfortunate assumptions, related with the extinction of *P. venusta* in the areas of Aguadores, Sardinero and Siboney (Santiago de Cuba province eastern plateau), which is not true. Tree snails such as *Polymita* and *Liguus* tend to live as a colony in patches throughout different ecosystems. This behavior was already noticed by J. B. Henderson in 1912, who wrote "...these creatures have a gregarious habit and live in colonies". Even in circumstances with optimal forest and host plants, you can find one or more colonies limited to very small areas consistently for several years. Tree snails are not motionless animals that only stop moving when they reach the forest fringe. We now know that they can travel through the litter and dirt in the rainy season, reaching and colonizing other nearby forest patches.

Thus, these hasty assumptions and conclusions tend to diminish any management actions and conservation strategies to protect this endangered land snail. In a forthcoming paper, we discuss new records of *P. venusta* populations in the Santiago de Cuba province plateau, and some fresh viewpoints on its actual distribution, threats and conservation challenges in this area.

ACKNOWLEDGMENTS

The authors thank Luis Dickinson Felipe, Rolando Teruel, and Noel Pérez Verdecia. Special thanks to our colleague and 'lucky charm' Yadira Sánchez Serrano, who was part of our field team when those populations were found.

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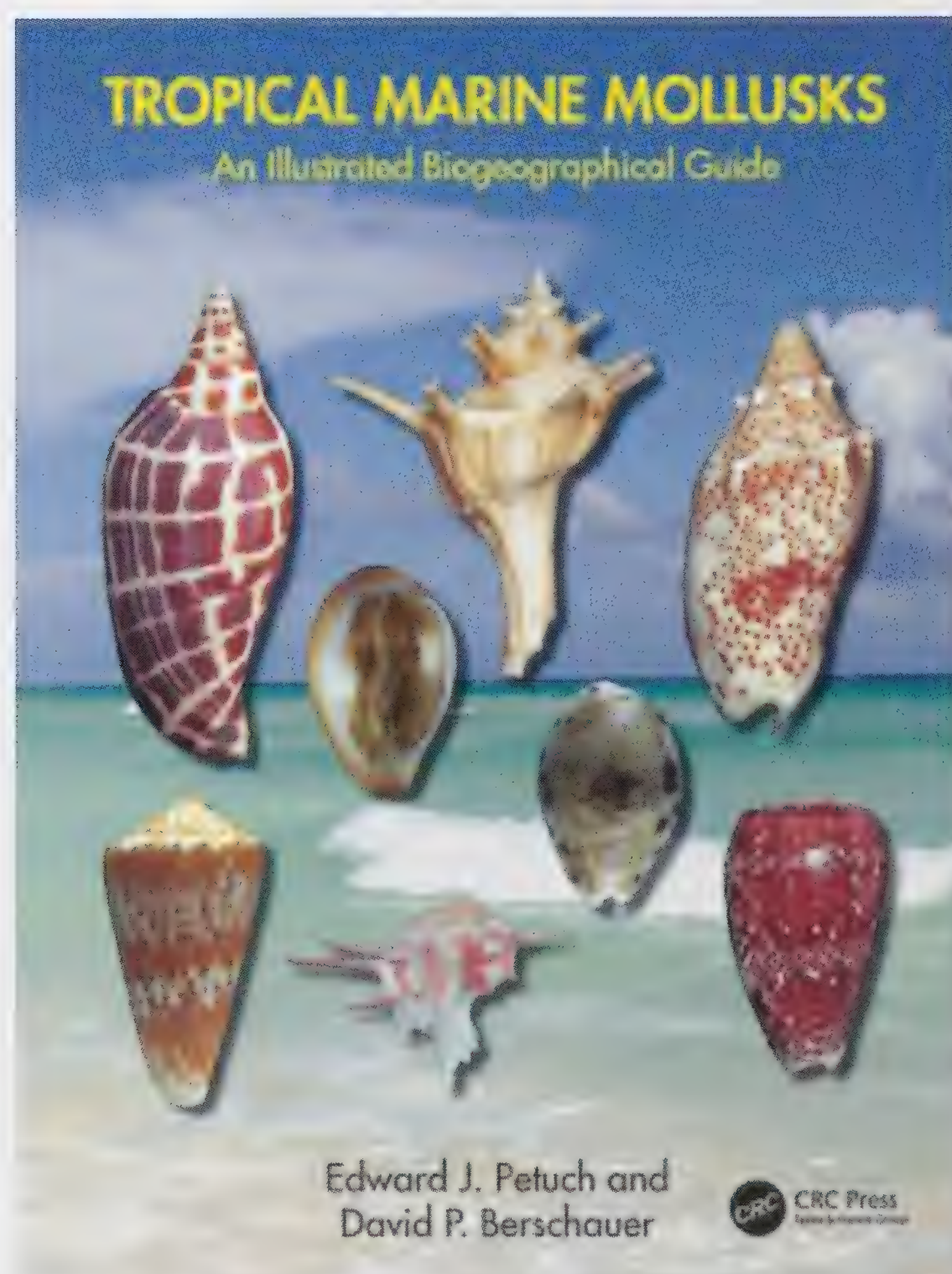
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Tropical Marine Mollusks - An Illustrated Biogeographical Guide

CRC Press - December 2020

Marine biogeography, the study of the spatial distribution of organisms in the world's oceans, is one of the most fascinating branches of oceanography. This book continues the pioneering research into the distributions of molluscan faunas, first studied by biologists over 160 years ago. It illustrates 1,778 species of gastropods in full color, many of which are extremely rare and poorly known endemic species that are illustrated for the first time outside of their original descriptions.

The spatial arrangements of malacofaunas shown in this book can be considered proxies for worldwide oceanic conditions and used as tools for determining patterns of Global Climate Change. The book's documentation of evolutionary "hot spots" and geographically restricted endemic faunas can also be used as a base line for future studies on patterns of environmental deterioration and extinction in the marine biosphere.

Documenting the evolution of the amazingly rich worldwide gastropod fauna, this book will appeal to physical and chemical oceanographers, systematic and evolutionary biologists, historical geologists, paleontologists, climatologists, geomorphologists, and physical geographers. The authors incorporate aspects of all of these disciplines into a new classification system for the nomenclature of biogeographical spatial units found in tropical, subtropical, and warm temperate seas.

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Figure 2. *Polymita venusta* morphs and host plants from El Tablón-La Estrella. *Erithalis fruticosa* (middle left), *Chrysophyllum cainito* (middle right) and *Comocladia platyphylla* (bottom left).



Figure 3. *Polymita venusta* morphs and host-plants from La Pollera-La Luz. Three morphs on *Bursera simaruba* (middle left) and light-yellow white banded form on *Smilax* sp. (upper right). Color variation named as *nigrosuturalis* was found only in this locality (upper, middle and bottom left pictures).



Figure 4. *Polymita venusta* morphs and host plants from La Cristina locality. Light-yellow morphs on *Vachelia macracantha* (upper left) *Euphorbia lactea* (middle left), and *Ipomoea violacea* (bottom).



Figure 5. *Polymita venusta* habitats in Sierra de Boniato. 1-2= La Cristina localities. 3-4= El Tablón-La Estrella locality, specimens were found both sides of the road. 5-7= La Pollera-La Luz locality.

Rejected Synonyms in MolluscaBase

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ABSTRACT A large number of new species in this author's books on South Asian shells have been designated as synonyms by Páll-Gergely *et al.* 2020, without convincing proof. In the last quarter of 2020 (*i.e.*, August-November), MolluscaBase (an Internet website that is a taxonomically-oriented database, in which B. Páll-Gergely is an Editor) rejected forty-one of this author's new species based on incorrect synonymization. This article distinguishes the differences between some of those new species and previously described species which have been synonymized, and utilizes photo comparisons to depict the inaccuracies of these designations.

KEY WORDS *Bouchetcamaena*, *Trichochloritis*, *Rhiostoma abletti*, *Tropidophora huberi*

DISCUSSION

1. *Rhiostoma abletti* Thach 2016 (Figure 1a). This species was designated as a synonym of *Rhiostoma marioni* (Ancey, 1898) (Figure 1b) by Páll-Gergely *et al.* 2020, without convincing proof to support that designation. There are seven key differences that distinguish *R. abletti* from *R. marioni*: (1) air tube much shorter and not touching the remaining shell; (2) transverse ribs not widely-spaced; (3) terminal part of body whorl broader (*i.e.* larger in diameter), not extended and not separated far from remaining shell; (4) outer lip not thick; (5) sutures shallower; (6) whorls less conspicuous; and (7) lateral side of body whorl (*i.e.*, opposite to the aperture) not strongly convex. It is regrettable that Páll-Gergely *et al.* did not detect these differences, or worse chose to ignore them. However, I would welcome a similar comparison providing evidence supporting their conclusions.

2. *Tropidophora huberi* Thach, 2018 (Figure 2a). This species was designated as a synonym of *Leptopoma annamiticum* Möllendorff, 1900

(Figure 2b) by Páll-Gergely *et al.* 2020, also without convincing proof to support that designation. As with *R. abletti* and *R. marioni*, there are seven key differences that distinguish *T. huberi* from *L. annamiticum*: (1) lack of spiral ribs; (2) absence of peripheral keel; (3) lower spire; (4) much larger umbilicus; (5) presence of broad brown spiral band at periphery; (6) not oblique aperture; and (7) a more inflated ventral side. In particular, the spiral ribs, shape of body whorl and peripheral keel are important features commonly used in the identification of these shells. However, Páll-Gergely *et al.*'s suggestion that this species differs from *L. annamiticum* only by a rounded body whorl (see page 40, at left column of their article) borders on sophistry. The seven distinguishing characters identified above are not difficult to detect, and it is disappointing that they appear to have been ignored. Again, I welcome a similar comparison by my colleagues providing evidence supporting their conclusions.

3. *Amphidromus yenlinhae* Thach & F. Huber, 2017 (Figure 3a). Here again Páll-Gergely *et al.*

2020 has synonymized two clearly distinguishable species, *A. yenlinhae* and *A. eudeli* Ancey, 1897 (Figure 3b) without providing convincing proof to support that designation. The shell characters of the *A. yenlinhae* differs from *A. eudeli* mainly in: (1) a more slender shape; (2) body whorl not swollen; (3) narrower and more pointed spire; (4) early whorls vivid red; (5) oblique stripes not interrupted at the middle as cited in original description (Ancey, C.F. 1897, in *The Nautilus* magazine); (6) outer lip white (*i.e.* not purple) and distorted at posterior end; (7) columella having different shape and not pale at upper part as cited in original description; (8) sutures having different color; and (9) aperture smaller with external pattern visible within. These nine differences easily distinguish the two species and it is inappropriate to suggest they are conspecific. As previously stated, I welcome a similar comparison by my colleagues providing evidence supporting their conclusions.

4. Genus *Trichochloritis* Pilsbry, 1891

Páll-Gergely *et al.* 2020, incorrectly moved the species *Helix fouresi* Morlet, 1886 (Figure 4a) to the genus *Trichochloritis* Pilsbry, 1891 as its shell characters are significantly different from those of *Helix breviseta* Pfeiffer, 1862 (Figure 4b); the type species of this genus. These differences include: (1) presence of a deep groove along periphery of body whorl; (2) much shallower sutures; (3) different ribs at dorsal side; (4) not inflated whorls; (5) smaller umbilicus; (6) not angulate columella; (7) lacking brownish band on body whorl at dorsal side; (8) not deformed aperture; (9) absence of dark-colored band along the suture of body whorl; and (10) different colors. These character differences are diagnostic and clearly place *Helix fouresi* in the genus *Bouchetcamaena*.

5. Genus *Bouchetcamaena* Thach, 2018.

Páll-Gergely *et al.* 2020, has designated this genus as a synonym of the genus *Trichochloritis* Pilsbry, 1891 without providing convincing proof. In fact, the type species of the latter has none of the distinguishing characters of the type species of the former. Figures 5 and 6 show the type species of *Bouchetcamaena huberi* Thach, 2018. Further, Figures 5a and 6a show that *Bouchetcamaena* is significantly different from *Helix breviseta* Pfeiffer, 1862 (which is the type species of genus *Trichochloritis*, see Figures 5b, 6b). Those two genera differ in the following characters: (1) translucent shell; (2) not inflated whorls; (3) different sculpture; (4) presence of flat area at the middle of body whorl at dorsal side; (5) umbilicus narrower and not funnel-shaped; (6) not angulate columella; (7) absence of brownish spiral band at dorsal side; (8) rounded (not deformed) aperture; (9) lack of dark-colored band along suture of body whorl and (10) different colors. Figure 5 shows four additional significant differences: (11) the presence of conspicuous peripheral keel; (12) lateral side of body whorl not convex; (13) aperture tilted forward at about 30°; and (14) inferior side of the shell is overhung by peripheral keel. These shell character differences easily distinguish these two genera. If Páll-Gergely *et al.* can show, by comparison photos, the similarities between these two type species it would be helpful in understanding their conclusions. In order to cast further doubt about the validity of this genus, these authors state that “the validity of the genus *Bouchetcamaena* can be verified when more material becomes available.” It is evident that any taxon (even the genus described by Páll-Gergely *et al.* 2020) can be revised or changed in the future based upon the acquisition and study of additional specimens. However, it is scientifically valid to maintain any genus as an official taxon until a more thorough study can be performed.

▲ After synonymizing forty-one taxa named by this author without serious conchological consideration and analysis, Dr. Barna Páll-Gergely published this author's book "New Shells of South Asia, Volume 2" on Facebook without verbal or written permission. This action sheds light on a more systemic problem that confronts our scientific community. When one allows their ego to cloud their judgement, it raises the question of whether that individual's research may be similarly clouded. Moral principles such as integrity, humility and respect strengthen our community and support the fundamental foundation on which science is based. When one of our colleagues disregards these principles, it places a shadow over our entire community and taints the knowledge we struggle to obtain for the benefit of Society as a whole. There are many issues in nature that are waiting to be investigated by malacologists, and while important, synonymization of taxa should not be their primary focus.

ACKNOWLEDGMENTS

The author thanks the Paris National Museum of Natural History for the photos of *Helix breviseta* and *H. fouresi*, the Brussels Royal Institute of Natural Sciences for the photo of *Amphidromus eudeli*, the London Museum of Natural History for the photo of *Leptopoma annamiticum* and the anonymous reviewers for their works on this article.

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Plate 1. Differential diagnoses shown on Figures 1 through 6 as marked.



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The San Diego Shell Club is interested in your shell collection. As a 501c(3) organization, all donations to our Club may provide a tax write-off. When we receive a donation we provide a letter describing the items that may be used when filing your taxes.

While we cannot provide a value, donations of up to \$5,000 do not require a written appraisal. Since tax laws change regularly we recommend that you check with your tax accountant before relying on any information provided here.

We are interested in all types of shells, marine or land and all genera and species, including books on shells as well as items related to shells such as artwork, storage cases and tools. Your donated items will be used to generate income to support the Club's efforts in continuing Public education about shells and conservation of marine life throughout the world. If you would like to donate, please contact David Waller, SDSC Acquisition Chairperson, at dwaller@dbwipmg.com to schedule a time to discuss charitable gifting.

CLUB NEWS

2020 November - General Meeting

Canceled due to the COVID19 pandemic.

2020 December - Holiday Party

Canceled due to the COVID19 pandemic.

2021 January General Meeting

Canceled due to the COVID19 pandemic.

President's Message

I've been asked to serve as the San Diego Shell Club's President for 2021, and it will be my pleasure to do so. I will have the pleasure to serve alongside a capable Board of Directors -- my "A" team. Before going any further, we are saddened to hear of the passing of one of our treasured Club members, DeWitt Rathbun. Who can ever forget DeWitt serving as docent, his enthusiasm telling his shell stories while manning the San Diego Shell Club's San Diego County Fair exhibit? DeWitt's presence will be sorely missed. Our condolences to Nan, DeWitt's wife.

When we look back, what will be said? It was the best of times, it was the worst of times. Ok, who's hiding the best of times? A doctor might prescribe something like - get out of our shell by getting back into our shells. Our sea shells. There's a need to reengage. Easier said than done, when trapped in this aggravating sort of standstill - warp. The task facing the Club, plain and simple, is the implementation of the needed remedy, which is a situation requiring adjustments, minor, major, however we choose to characterize the coming developments. And truth is, someday we'll look back noting that the Club needed a not-so-gentle push, and that it had been in past time to make a necessary foray into the virtual reality future. Indeed, we may ask what took so long? Answer: the need for empowerment. Tolkien wrote of necessity being an empowering thing, which has some pertinence for today. The Club's future is no longer on the horizon. Currently, the Club's board meetings are Zooming. Next is Zoom general meetings, then virtual auctions. We'll see. Certainly next will be something even better, and so on, from here on out, transitioning the Club into an ever-brighter virtual future. We hope. If Zooming it's to be, then to the rescue we have Zoom Man and Robin: Dung Vo and Robyn Waayers. If not Marvel characters, marvelous solutions for the Club's virtual needs. And yes, we've all been watching too many movies.

The SDSC questionnaire. Please, if you haven't done so, your response to Robyn's important questionnaire would be appreciated, while you have the time. While Robyn is tallying the opinions, please add your own two cents to the interesting responses. More on the future direction of our Club's publication will come from Club Editor, David Berschauer, so stay tuned. Speaking of your two cents, dues have been sent in? Check that box. And if you're reading this and you haven't sent in your dues yet, you've been given a reprieve, in which case free up some of that stimulus cash. Sending in your dues early helps the Club tremendously.

During these transitional times, something for us not to lose sight of while exploring for solutions in a future virtual world is just that -- exploring. And discovery, education and learning -- teaching. Seems I recall somewhere mention of such things. Our raison d'être. Our Club mission statement perhaps? Mentally, I'm adding shell collecting to the list, noting logically that the greater the interest and subsequent value, the greater the likeliness that we preserve and protect. It's the way it works. We suggest that Club members be current on all Club details by familiarizing themselves with the Club website. Because to have a future, you must get there. Don't get waylaid by micro adjustments. And we'll try to keep changes and cancellations to a minimum. In closing, the San Diego Shell Club's Board of Directors wishes all of you health and prosperity in the coming year. And we pray that our valued members and their families stay well during these trying COVID times.

Cheers,
Laurence Buck



P.S. Me and Johnny. John Jackson and myself. Drive trip. San Miguel Island circa a hundred years ago. A teaser. You'll find out later.

Editor's Corner - how rebuttal papers help science

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As a scientific research community, it is important that we are able to communicate in a way that promotes the advancement of our particular field of study. While we may not agree with a colleague's work, it is incumbent upon each of us as a member of that community to investigate and provide evidence to either support or reject conclusions presented by others. In addition, when communicating our findings, it is important to do so in a professional manner consistent with the requirements of science. This article provides an example of that professionalism.

An article was published in the August 2014 Festivus (45(4): 86-89) titled "Review of "Two Extremely Rare Australian Fossil Cowries" (GASTROPODA: CYPRAEIDAE)" by this author. The article addressed some of the conclusions presented by F. Lorenz in his 2009 article on *Umbilia gastrolax* (Acta Conchyliorum, 10:83-86). In that article, Lorenz notes that the dorsum and upper surface of the flange are glossy and concluded that the animal's mantle must have covered these surfaces. However, the extreme angles present in the shell's morphology raised the question of whether the mantle was flexible enough to conform to the areas indicated by the arrows in Figures 1 A-B. Could it be that the glossy appearance of the dorsum was residual from before the flange was created and could the glossy surface of the upper portion of the flange merely be the result of its creation?



Figure 1. (A) shows the extreme angle between the dorsum and the flange and (B) shows the extreme narrow perimeter edge.

Lorenz's article further speculated that the flange was an adaptation that increased the basal surface area of *U. gastrolax* allowing it to better survive on soft muddy bottom environments; a conclusion based on the composition of the matrix in which this fossil was extracted. This was certainly a possibility. However, could it have been an adaptation used to protect its eggs or brood from predation and if that were the case, could the flange have been created after the animal became reproductively active? In my article, I proposed looking at a cross-sectional view of the flange

including where the flange meets the base of the shell to answer these questions. Diagrams were presented (see Figures 2 and 3, reproduced below from *The Festivus* 45(4):86-89) showing the expected deposition of nacre and shell material for each case.

Figure 2. Diagrammatic representation of a cross-section of the flange showing the anticipated enamel deposition if the mantle covered both sides of flange (A) and only the bottom side of the flange (B).

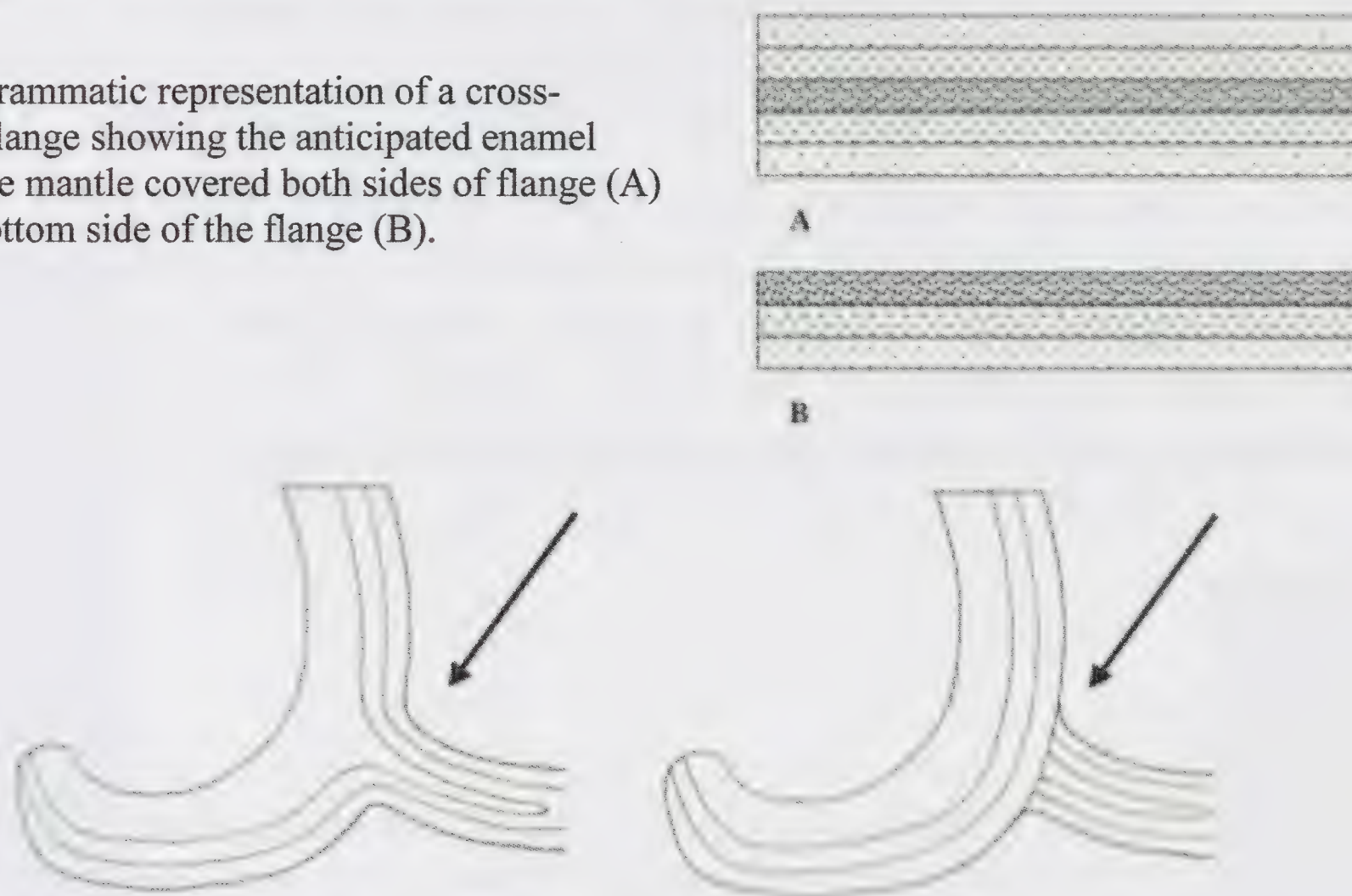


Figure 3. Diagrammatic representation of a cross-section of the flange extending from the margin showing the anticipated enamel deposition if the flange was created at the time the base was formed (A) or after (B).

Lorenz may have seen my article or had considered answering these questions as well. His results were published in volume 2 of “*Cowries; A Guide to the Gastropod Family Cypraeidae*” published in 2018 (see page 682, Plate 337). Lorenz provides a micrograph of a cross sectional view of the flange showing the external and internal layers of the shell. These layers are similar to those shown in my article demonstrating that the mantle did cover the upper portions of the flange and dorsum and were not later added at maturity but were a part of the progressive development of the shell.



I was pleased to see that Lorenz addressed these questions. The author's suggestion of viewing a cross-section of the flange and side of the shell was able to show that the mantle did cover the top of the flange and dorsum. Further, it seems to show that the flange was present during development and not created later in life (see above, Figure 7 from “*Cowries; A Guide to the Gastropod Family Cypraeidae*” Volume 2).

Musings on some self-collected shells from San Diego County

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In 1977, my family moved from the Delmarva Peninsula on the east coast to San Diego. I had started to get the shell bug as a child in the east, and, equipped with little more than the Golden Nature Guide to Seashores (as shown in Figure 1 below) and a few library books, tried to identify my beach finds, especially from Ocean City, Maryland (see Figure 2 below). I kept the “best” specimens (which were badly wave-worn) and marveled at shells in the local shell shops from that mythical place, “California”.

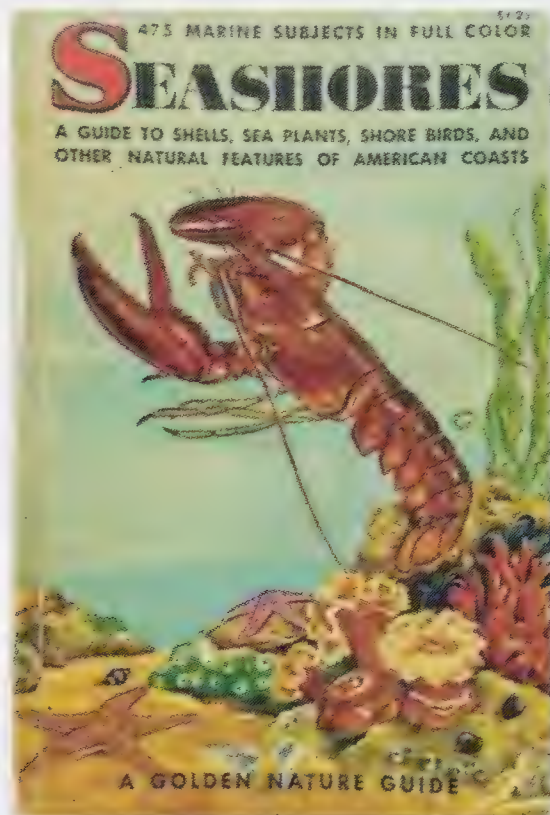


Figure 1. Seashores: A Guide to Shells, Sea Plants, Shore Birds, and Other Natural Features of American Coasts by Herbert S. Zim and Lester Ingle. My first enticing images of sea creatures were in this compact little treasure.



Figure 2. A view of Ocean City, Maryland, from the south, looking north. This little strip of land seemed like a shell bonanza for me as a child.

Then, seemingly, a miracle occurred, and we actually moved to that mythical place. Somehow, we acquired the Peterson “A Field Guide to Pacific Coast Shells” by Morris (as shown in Figure 3 below) and now, as my interest in biology was blossoming, I avidly read the introduction with its descriptions of how to build a good local shell collection, including even how to label and store one’s finds. Briefly, I imagined going all in on such an effort, but as a young teen, my interests wavered, and after collecting a handful of local specimens, I drifted into other interests (as it turned out, for several decades).

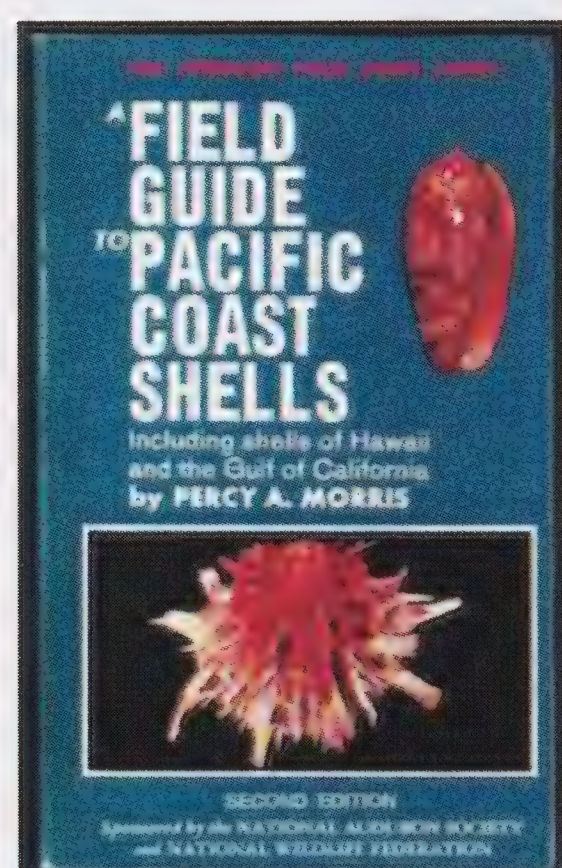


Figure 3. A Field Guide to Pacific Coast Shells Including Shells of Hawaii and the Gulf of California by Percy A. Morris. My bible for a while after the family settled in San Diego.

Around 2014, I got to thinking about shells again and realized that I could finally collect them “seriously”, and store them properly in high quality cabinets, as I’d dreamed of so many years previously. So back to the local beaches I went, searching for southern California shells.

Over the past five years or so, I’ve built a modest but respectable collection of common local species, but have also found a few somewhat more special or interesting specimens. A couple of these specimens have been written about in previous issues of *The Festivus*.

This article is meant to summarize some of my more intriguing shell finds on local beaches. At least one still remains a mystery as far as its identity, so perhaps wider exposure in this article will help solve that mystery.

Many times over the years, I had read about tusk shells as if they were common here in California. Any organism used as “money” (as native peoples here did in the past) must surely be pretty abundant. But I never found even one tusk shell back in the late 1970s and early 1980s at local beaches or tidepools.

Then in January of 2014, I found a single empty *Dentalium neohexagonum* Sharp & Pilsbry in Pilsbry & Sharp, 1897 on the sand at low tide just south of what used to be referred to as False Point (just north of Pacific Beach). It is shown in Figure 4, A below.

Then a month later in February of 2014, I found around a dozen of the other scaphopod species of the region, *Antalis pretiosa* (Sowerby, 1860) on the beach south of Imperial Beach. The shells were all washing up around near the water line at a low tide (see Figure 4, B for the largest specimen).

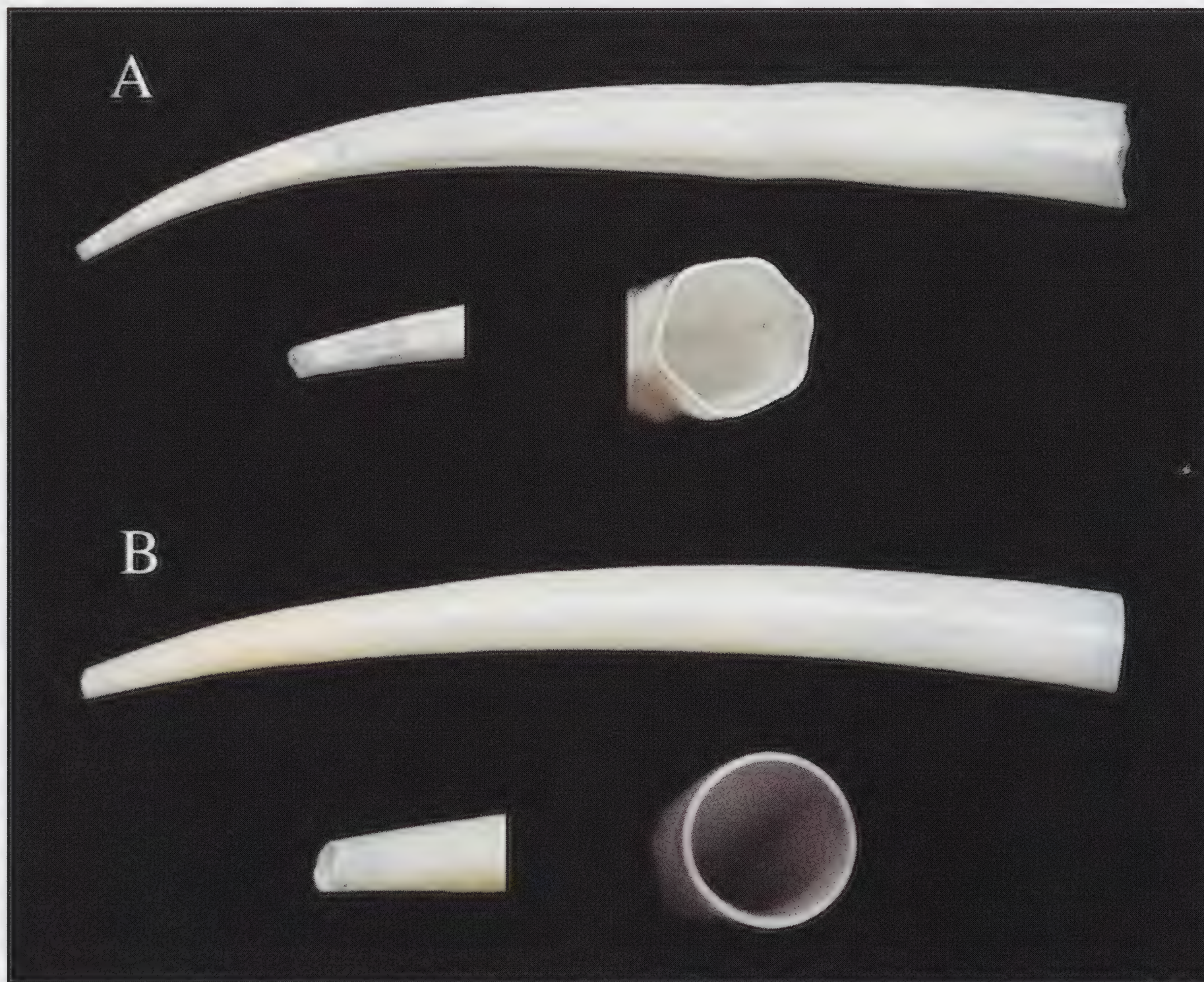


Figure 4. Self-collected Scaphopoda from San Diego County. **A**= *Dentalium neohexagonum* Sharp & Pilsbry in Pilsbry & Sharp, 1897, 23 mm. and **B**= *Antalis pretiosa* (Sowerby, 1860), 36 mm.

Note: Images not to scale.

There are many bivalve species occurring locally and some can be found washed up in decent condition following storms, or just at low tides.

Some of the more interesting bivalves that I have found on our local beaches include those shown in Figure 5. *Amiantis callosa* (Conrad, 1837) is a large and elegant venerid clam, sometimes washed ashore intact. My best specimen is from south Coronado (north of Imperial Beach), shown in Figure 5, A. Both its valves are present, and the hinge is in good condition. The delicate periostracum is the only thing missing. This stretch of beach is very pleasant to beach-comb on, by the way, and seems to constantly change with regard to the species washed up on it.

Mission Bay is a surprisingly productive place for local shelling, especially at low tide. Actually getting in the water (in my case, by snorkeling) widens the collecting horizons even more. Pectinids (scallops) are not so easy to find intact if one does not dive, but at very low tides in Mission Bay there are several species that can be found washed ashore. An unusual pectinid that I found in Mission Bay is a smallish specimen of *Leopecten diegensis* (Dall, 1898), a species not normally seen

washed up in this location (Figure 5, B). The two valves were on the surface of mud on the north end of Vacation Isle at a very low tide. I almost ignored them, but luckily then looked again!

The small scallop *Leptopecten latiauratus* (Conrad, 1837) is quite commonly seen in Mission Bay, and in February of 2015, I found a scallop that superficially resembled an orange form of *Leptopecten latiauratus* (Figure 5, C). But upon asking for help with its identity, it did not seem to match that species. Ultimately it was sent to the bivalve specialist Paul Valentich-Scott at the Santa Barbara Museum of Natural History and his determination was that it was a slightly deformed specimen of *Leptopecten camerella* (Berry, 1968), a species normally found in Mexico.

My last “interesting bivalve” here is an intact specimen of what I think may be *Modiolus rectus* (Conrad, 1837) as shown in Figure 5, D. This is a nice large mytilid (mussel), which I have seen washed ashore both north and south of Imperial Beach. Usually the specimens are damaged, but I do have one decent specimen from just north of the Tijuana River mouth found in April of 2014 following very high tides.

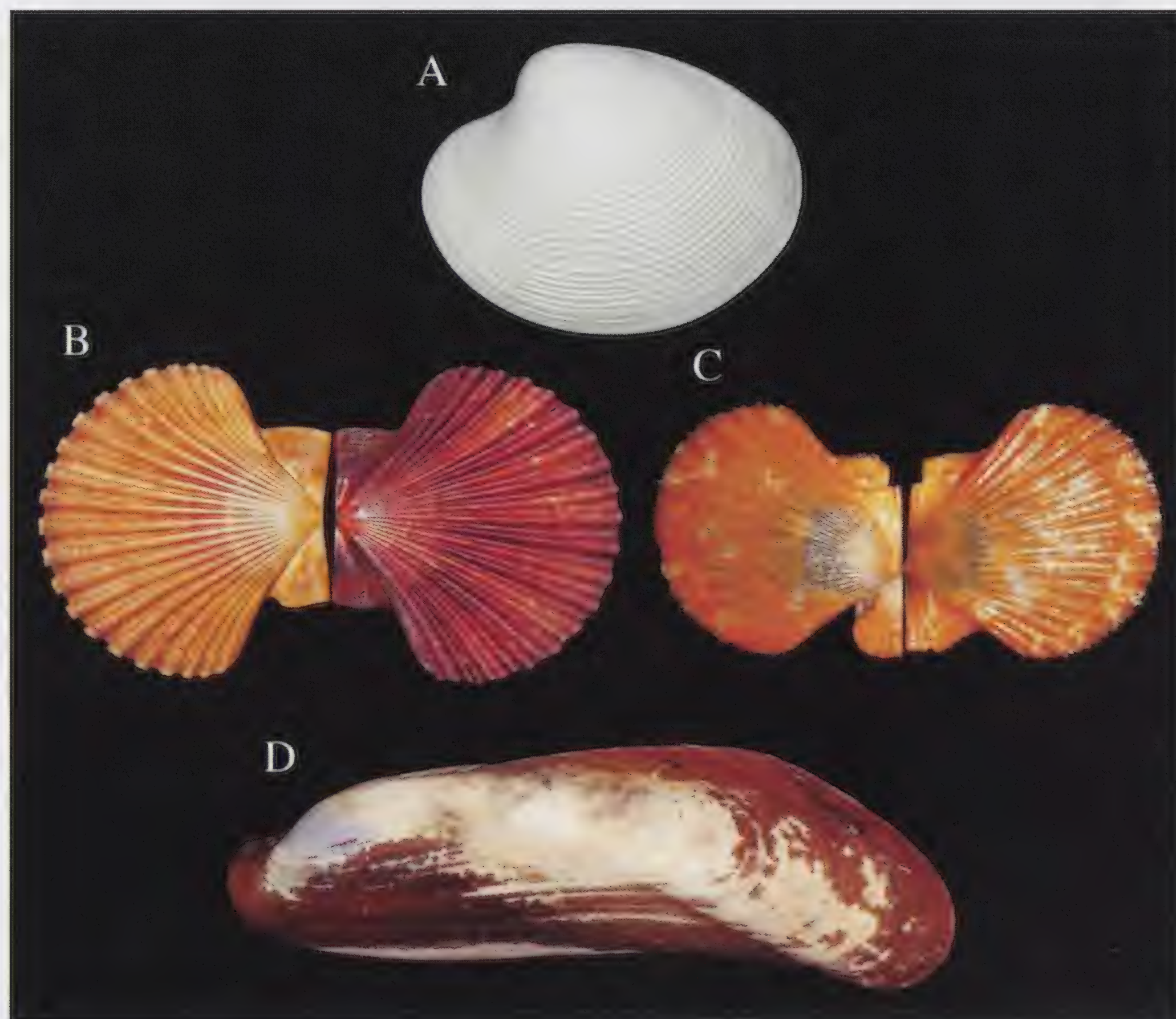


Figure 5. Self-collected Bivalvia from San Diego County. **A**= *Amiantis callosa* (Conrad, 1837), 80 mm. **B**= *Leopecten diegensis* (Dall, 1898), 50 mm wide. **C**= *Leptopecten camerella* (Berry, 1968), 17 mm and **D**= Likely *Modiolus rectus* (Conrad, 1837), 152 mm. Note: Images not to scale.

Our local gastropods are numerous and fun to search for, but I am only showcasing a handful of what seemed to be “unusual” species, at least to me (Figure 6). At extreme negative low tides, I have found specimens of the moderate-sized snail, *Burchia semiinflata* (Grant & Gale, 1931), formerly known as *Crassispira semiinflata* (Grant & Gale, 1931) on Vacation Isle in Mission Bay (Figure 6, A). They burrow in the sand but are often visible as lumps or are partially exposed. December of 2016 seemed to be a good time for them.

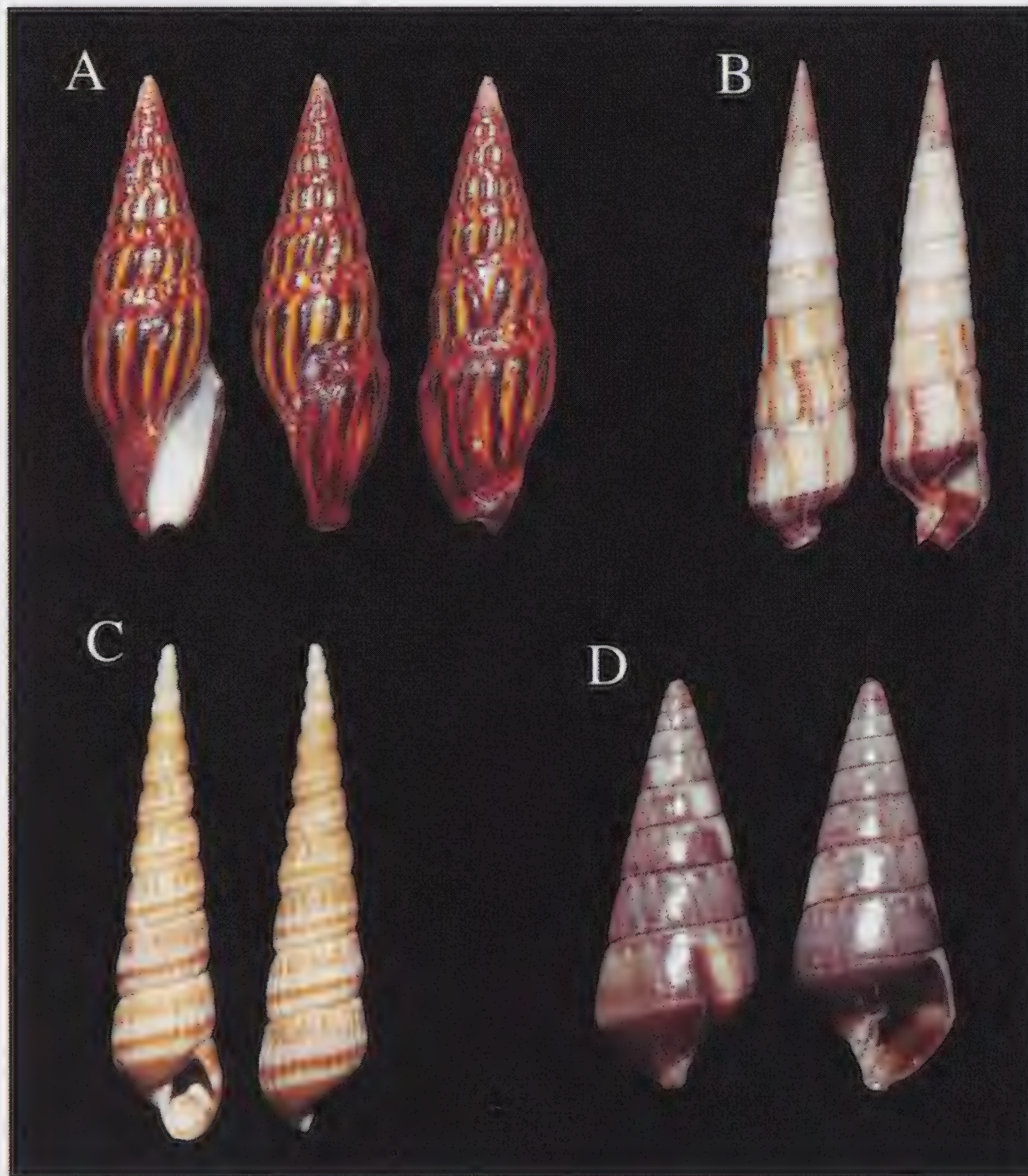


Figure 6. Self-collected Gastropoda from San Diego County. **A=** *Burchia semiinflata* (Grant & Gale, 1931), 41 mm. **B=** *Terebra pedroana* Dall, 1908, 38 mm. **C=** *Turbonilla macouni* Dall & Bartsch, 1910, 14 mm and **D=** *Pyramidella adamsi* Carpenter, 1864, 8 mm. Note: Images not to scale.

Another gastropod that I have only observed once was also found on Vacation Isle in Mission Bay – *Terebra pedroana* Dall, 1908 (Figure 6, B). The combination of low tide and a sharp eye on the sand yielded this elegant little terebrid.

And not to be outdone, the tiny shells – maybe not truly “micro” but still not exactly large ... *Turbonilla macouni* Dall & Bartsch, 1910 is a seldom-seen species, and scrounging around in the shelly debris in a catch basin south of Imperial Beach yielded a single specimen in February of 2014 (Figure 6, C).

A second member of the Pyramidellidae, along with my *Turbonilla macouni* is *Pyramidella adamsi* Carpenter, 1864, a specimen of which I found, yes...on Vacation Isle, Mission Bay (Figure 6, D)! Needless to say, this is a nice shelling location, especially if one patiently waits for extreme low tides and searches very carefully.

I also have a mystery gastropod, a moon snail (family Naticidae), found (again) on Vacation Isle. It was an empty specimen found at South Cove at a low tide (Figure 7). It does not seem to match expected species of this family in the area and I have had no luck with determination at this date. Help with identification of this shell would certainly be welcome!



Figure 7. Self-collected undetermined naticid, 30 mm. South Cove, Vacation Isle, Mission Bay, San Diego, California. Collected January 10, 2017.

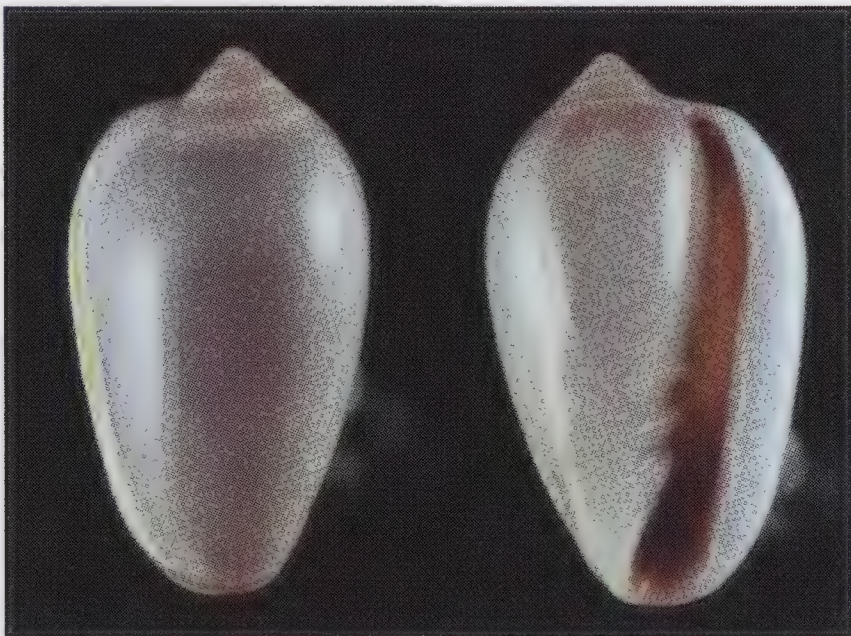
Speaking only for myself, I would say in summarizing the best places to search for shells in San Diego County, that the locales turning up repeatedly in this article are certainly good for shells ... at the right times. Low tides tend to be most productive, especially the negative ones in winter and summer. I've had good luck in many spots in Mission Bay, though (other than the ones described) including Ventura Cove, Mariner's Basin and Crown Point. North Pacific Beach/southern La Jolla are good beach-combing locales also, especially at low tides following storms. And the south county is very rich also.

If you want to find some interesting local shells, consider equipping yourself with the San Diego Shell Club's "Marine Shells of the California Province" and keep in mind, the more you're out looking, the more you'll find! Happy shelling!

**Additional Paratypes of a Population of
Prunum sunderlandorum Petuch & Berschauer, 2020**

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Kevan and Linda Sunderland collected the type lot of *Prunum sunderlandorum* Petuch & Berschauer, 2020, consisting of 28 specimens on a trip to Honduras in 1987. Recognizing that this small Marginellid may be a new species they selected seven specimens from the lot which they collected and provided them to Dr. Edward Petuch for study. During our work on the paper I examined and photographed the shells. One specimen of the seven shells which were examined by the authors was chosen to be the holotype, and is now lodged with the Los Angeles County Museum of Natural History as LACM 3802. The Sunderlands retained the remaining 16 specimens from the original lot, which are illustrated herein; the lengths of these specimens are also listed.



Holotype LACM 3802



Holotype: 12.6 mm in length

Petuch Collection: lengths

P1 11.3 mm
P2 12.4 mm

Berschauer Collection: lengths

P3 11.7 mm P4 11.6 mm
P5 11.5 mm P6 12.3 mm

Sunderland Collection paratype specimens: lengths

P7 11.8 mm	P15 11.4 mm
P8 11.3 mm	P16 11.5 mm
P9 13.1 mm	P17 11.7 mm
P10 12.0 mm	P18 12.3 mm
P11 12.4 mm	P19 12.0 mm
P12 12.6 mm	P20 12.5 mm
P13 12.3 mm	P21 12.0 mm
P14 12.5 mm	P22 12.6 mm



E. adansonianus adansonianus (Crosse & Fischer, 1861), Bahamas, 106.1 mm. *B. poppei* (Anseeuw, 2003), Tonga Islands, 58.8 mm. *P. amabilis f. maureri* Harasewych & Askew, 1993, USA, 42 mm. *B. tangaroana* (Bouchet & Métivier, 1982), New Zealand, 55.9 mm. *P. quoyanus* (Fischer & Bernardi, 1856), Curaçao, 50.7 mm. *B. philpoppei* Poppe, Anseeuw & Goto, 2006, Philippines, 65.1 mm. *B. charlestonensis* Askew, 1987, Martinique, 77.3 mm. *B. midas* (Bayer, 1965), Bahamas, 82.7 mm.

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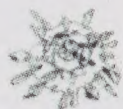
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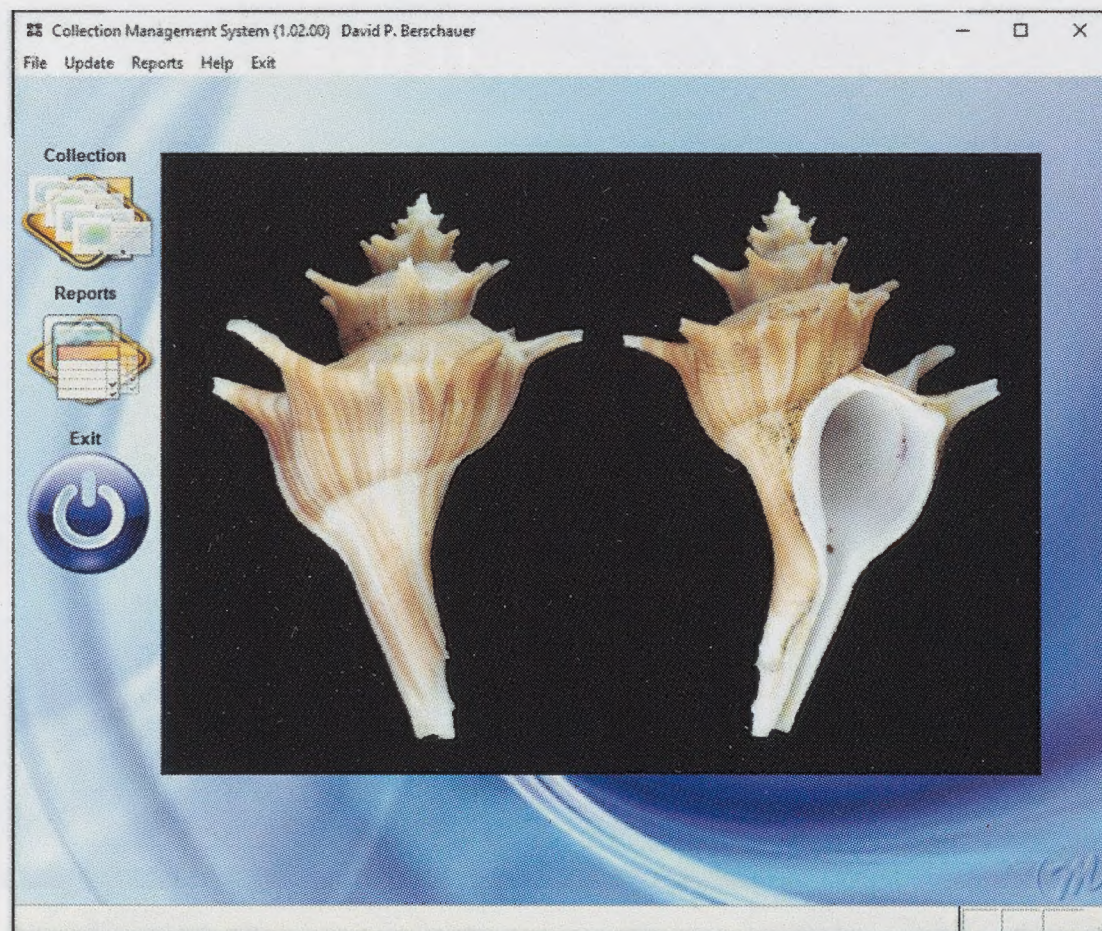
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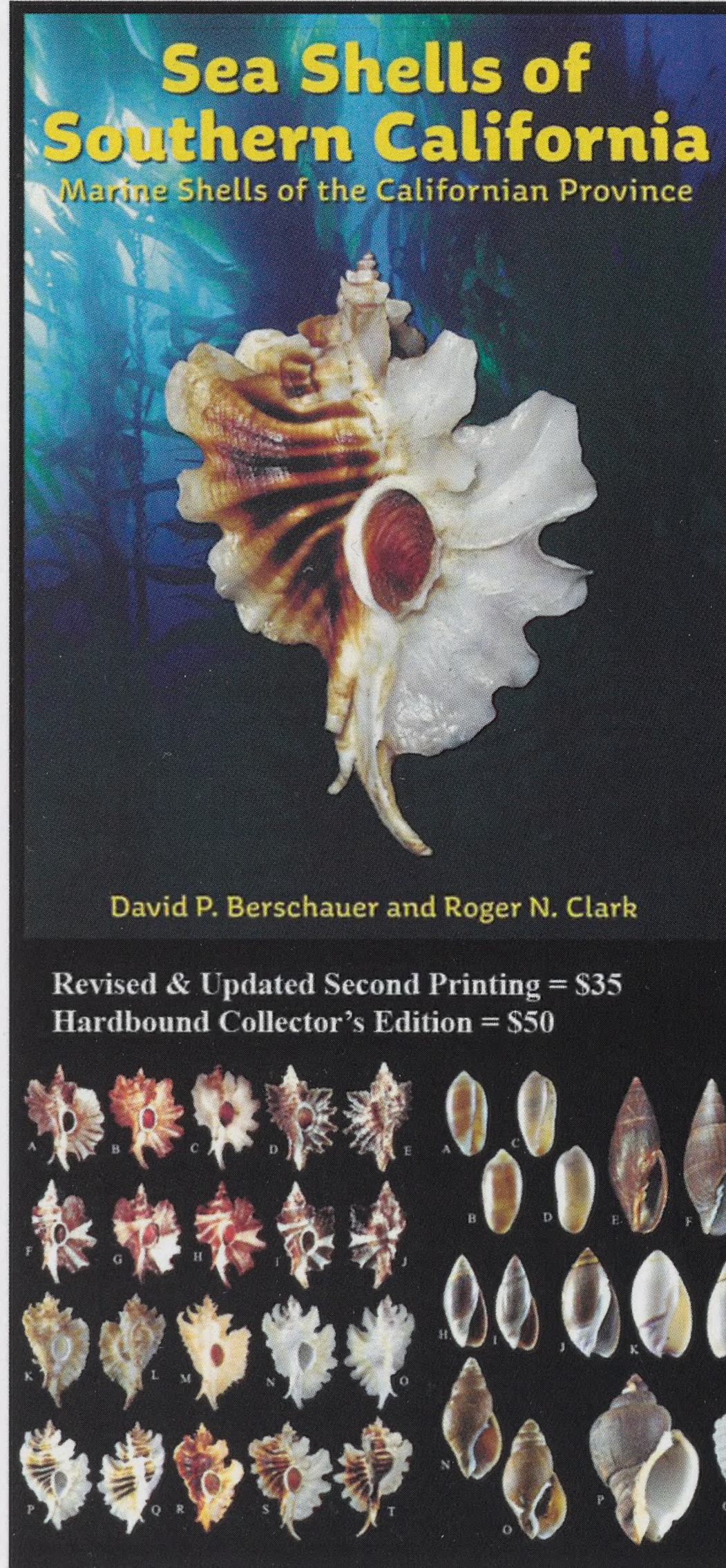
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Back cover: Fossil *Cassis* species aka "helmet shells" *Cassis viliusi* Petuch and Berschauer, 2021 (new species named in this issue of The Festivus), *Cassis jameshoubrieki* Petuch, 2004, and *Malea springi* Petuch, 1989, artistically arranged with medieval helmets. (Cover artistic credit: Rex Stilwill)

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